PHYLOGENETIC SYSTEMATICS AND EVOLUTION OF THE GAUDY GRASSHOPPER FAMILY PYRGOMORPHIDAE (INSECTA: ORTHOPTERA)

A Dissertation

by

RICARDO MARIÑO-PÉREZ

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Chair of Committee,	Hojun Song
Committee Members,	Gregory A. Sword
	Spencer T. Behmer
	Kevin W. Conway
Head of Department,	David W. Ragsdale

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ABSTRACT

The family Pyrgomorphidae, also known as gaudy grasshoppers, is one of the most colorful families of Orthoptera in the world. It is composed of 487 species in 149 genera and is particularly diverse in the Old World. Many members of this family are economically important pests, and some are culturally important as food for humans. Nevertheless, this family has not been well studied from the phylogenetic perspective. The objective of this dissertation is to modernize the systematics of Pyrgomorphidae. I provided a review of a taxonomic history of the family and information about type depository, and created 12 illustrated regional keys covering all the 149 Pyrgomorphidae genera of the world. Then, the first phylogenetic hypothesis for the family based on morphology was conducted to test the monophyly of the family and subfamilies. Regarding the origin of the New World Pyrgomorphidae, the entire mitochondrial genome and four nuclear genes were used to test different hypotheses about its origin and I found that they colonized South America from Africa in two waves, in ~95 and ~70 mya, and later diversified to the Caribbean, Central and North America. Furthermore, with the most comprehensive taxon sampling (105 out of 149 genera) and additional morphological evidence, the previous classification scheme was tested for the first time in a phylogenetic framework. From both morphological and molecular evidence, the family was recovered as a monophyletic group but the subfamilies were recovered as paraphyletic. The evolution of wings was studied in a phylogenetic framework, which showed that wing loss occurred multiple times across the family. Regarding aposematism and chemical defense, the analysis found that different modes of chemical defense evolved separately from each other. This dissertation represents a solid foundation and cornerstone for the systematics of Pyrgomorphidae.

DEDICATION

To my family

To Dr. Ignacio Bolívar y Urrutia and Dr. Keith McE.Kevan

Dicebat Bernardus Carnotensis nos esse quasi nanos, gigantium humeris insidentes, ut possimus plura eis et remotiora videre, non utique proprii visus acumine, aut eminentia corporis, sed quia in altum subvenimur et extollimur magnitudine gigantea

—John of Salisbury, *Metalogicon* (1159)

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Contributors

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All work for the dissertation was completed independently by the student.

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CHAPTER I

INTRODUCTION

The family Pyrgomorphidae is well known among orthopterologists because it has been studied for centuries due to its abundance, size, and bright coloration of certain species. Currently, there are 487 recognized species in 149 genera (fig. 1.1). The first five species were described by Linneaus between 1758 and 1771 and the very last eight species were described in 2017. There are still more species to be discovered, but in general, the family diversity is well documented. They are distributed mainly in the Old World with some representatives in the New World.

The aim of this dissertation is to modernize Pyrgomorphidae systematics in an explicitly phylogenetic framework. This dissertation consists of the following seven chapters. Chapter 1 provides an introduction to the family with some key aspects of its biology that will be discussed in a phylogenetic framework in later chapters. It also discusses economical and cultural significance of this family. Chapter 2 consists of a systematic review of the Pyrgomorphidae, which includes a taxonomic history and type depository information for all currently valid species and subspecies with an analysis of the main collections worldwide holding type material. Chapter 3 presents the comprehensive identification keys to the Pyrgomorphidae genera of the world, which has been compiled for the first time in the same language and profusely illustrated, consisting of 12 regional keys. Chapter 4 presents the first phylogenetic hypothesis for the family based on morphology, which tests the monophyly of the family and subfamilies. Chapter 5 uses entire mitochondrial genome and four nuclear genes to elucidate the origin of the New World Pyrgomorphidae and tests previous hypotheses regarding the origin from the Old World for the first time in a phylogenetic framework. Chapter 6 combines both new morphological evidence and a comprehensive taxon sampling of the

family to unveils the tribal relationships, proposing a phylogeny-based natural classification system and to understand the evolution of aposematism and wings in a phylogenetic framework. Finally, Chapter 7 summarizes all the previous chapters into a conclusion with perspectives and future directions.

Figure 1.1. *Maura lurida* (Africa).

1.1 Definition of Pyrgomorphidae

The family Pyrgomorphidae (Orthoptera: Caelifera) contains some of the most colorful grasshoppers in the world (which is why they are also known as gaudy grasshoppers). Currently, there are 487 valid species in 149 genera in this family. The family is distributed mainly in the Old World, but there are several genera known from Mexico and South America as well as Australia (fig. 1.3). Pyrgomorphs are easily diagnosable by the presence of a groove in the fastigium of vertex (Kevan & Akbar, 1964) and very distinctive phallic characteristics such as the cingulum extending around to the ventral side, the endophallic apodemes turned medially, and the ejaculatory sac open to the genital chamber (Eades & Kevan, 1974; Eades, 2000) (fig. 1.2).

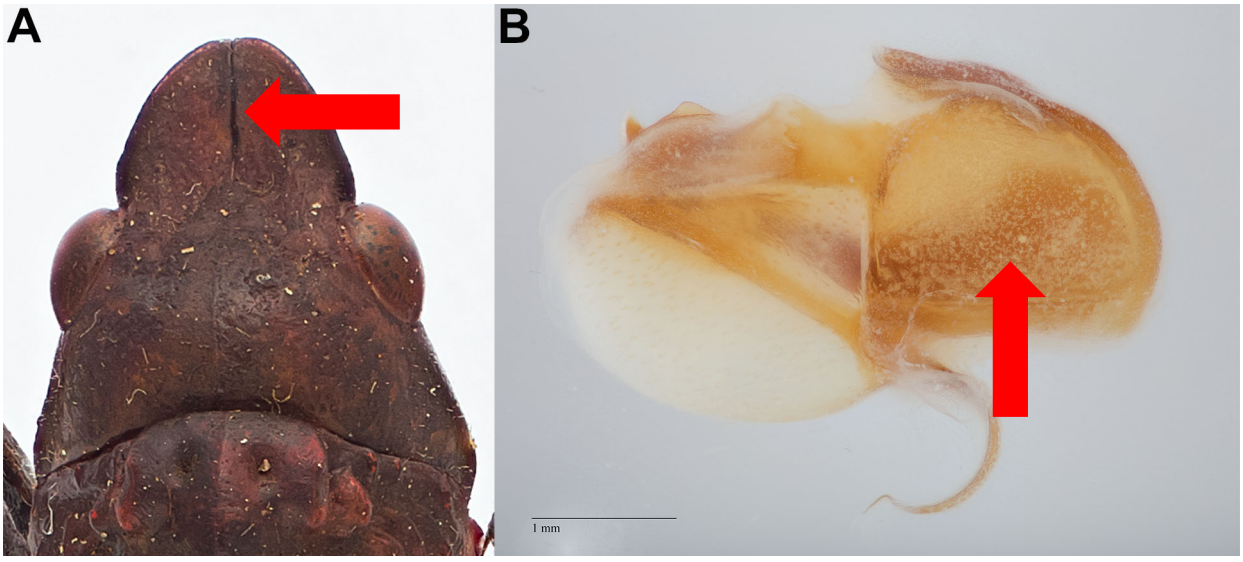

Figure 1.2. Main morphological characteristics defining Pyrgomorphidae. **A.** Groove in the fastigium of vertex. **B.** Cingulum extending around the ventral side (right).

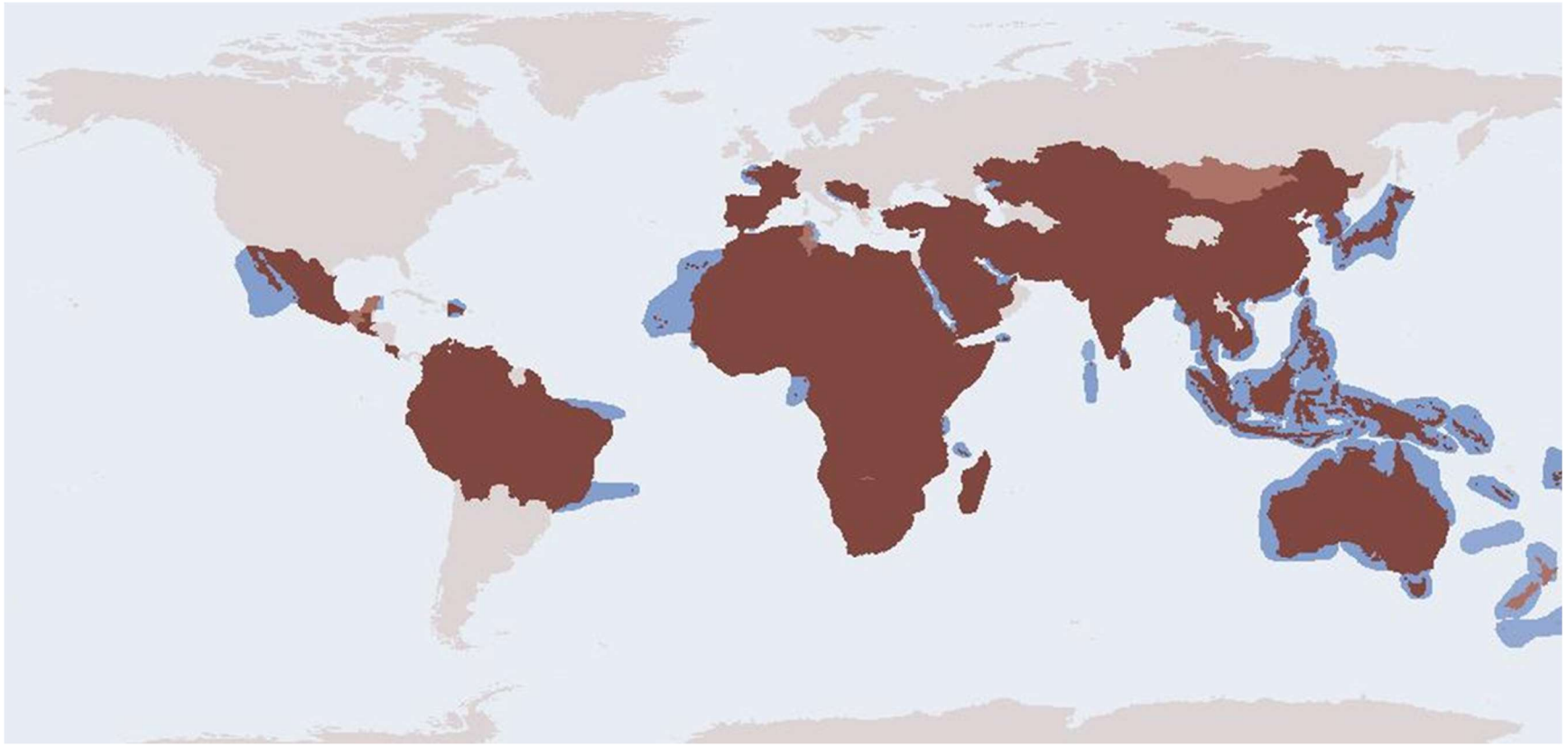

Figure 1.3. Distribution of Pyrgomorphidae based on Orthoptera Species File (Cigliano et al., 2018).

1.2 Interesting aspects of the biology of Pyrgomorphidae

1.2.1 Wing polymorphism

The family Pyrgomorphidae includes species with different levels of wing development from apterous (wingless) to fully winged, passing through micropterous (presence of tegmina but non-functional that is, unable to open) and brachypterous (tegmina reduced but still able to open). There are some species, which possess wing polymorphism even in the same population, such as *Rubellia nigrosignata* (Madagascar) (fig. 1.4A,B), *Yeelana argus, Monistria pustulifera, M. discrepans, M. latevittata, Psedna nana* (Australia), *Chrotogonus hemipterus* (fig. 1.4C,D), *Maura rubroornata* (fig. 1.4E,F), *Zonocerus elegans,* and *Z. variegatus* (Braud et al. 2014; Rentz et al. 2003; Rowell et al. 2015). Basically, wing polymorphism represents a classic life history trade-off, which involves one morph (short-winged or wingless) unable to fly but able to produce more eggs than its counterpart morph (long-winged) which can use its wings for dispersal, but with a reduction in reproductive output (Zera & Brisson, 2012). For decades, the studies on wing polymorphism (short-winged morph vs long-winged form) has focused in a role of juvenile hormone (JH), and recently it was found that a novel morph-specific JH titre circadian cycle (working in long-winged form but not in short-winged form) is involved in the maintenance in wing polymorphism using crickets as a model system (Zera, 2016). However, it is not known that the same JH-mediated mechanism is involved in Pyrgomorphidae.

Figure 1.4. Wing polymorphism in Pyrgomorphidae. **A.** *Rubellia nigrosignata* brachypterous. **B.** *R. nigrosignata* macropterous forms (Madagascar). **C.** *Chrotogonus hemipterus* micropterous form. **D.** *C. hemipterus* macropterous form (Mozambique). **E.** *Maura rubroornata* brachypterous form. **F.** *M. rubroornata* macropterous form (South Africa).

1.2.2 Chemical defense

1.2.2.1 Mid-dorsal abdominal gland

Grasshoppers have evolved multiple defensive mechanisms against predators, such as autotomy (ability to break off limbs) and chemical defense. Among the chemical defenses, there are several modes including regurgitants (commonly known as tobacco juice, or gut-mediated defense), glandular secretions, and internal toxins (Whitman, 1990). It appears that glandular secretions in particular seem to have evolved at least three times within Acridomorpha: 1. Mid-dorsal abdominal glands in Pyrgomorphidae; 2. Metathoracic tracheal glands in Romaleidae, and; 3. Eversible pronotal glands in Oedipodinae (Acrididae). Glandular secretions are exocrine defensive glands that discharge highly repugnant substances (such as cardenolides and pyrrolizidine alkaloids) when both nymphs and adults are disturbed, and often involve an arched stance to increase hemostatic pressure. Usually, hemolymph is also released but does not originate in the gland itself. Frequently these secretions are accompanied by hissing noise (Whitman, 1990).

In the case of Pyrgomorphidae, these mid-dorsal abdominal glands have been recorded in the African and Asian representatives, such as *Phymateus, Phyteumas*, *Poekilocerus*, *Zonocerus,* and *Colemania* (Whitman, 1990).

Coleman (1911) reported a gland in *Colemania sphenarioides* (India) that opens between the first and second abdominal segment, which secretes a slightly yellowish, milky liquid with a peculiar odor that appears to be repugnant and that can be ejected as far as 1-2 inches. Pavlowsky (1916) found a gland in *Phymateus aegrotus* (Kenya) in the wall of the first and second abdominal segment. The secretion becomes foamy when mixed with air. He also found two more

glands between the second and third abdominal segments which secrete substances in the form of grains. Hingston (1927) reported emission of fluid between the first and second abdominal segments in *Poekilocerus pictus* from India and found differences of the ejection of the fluid between nymphs and adults due to the presence of wings in the adults. De Lotto (1950) collected *Phymateus viridipes* and *P. pulcherrimus* in Eritrea and observed a white, milky nauseous liquid, which reminded him of the odor of the leaves of *Datura stramonium*. This liquid was secreted by a gland (5.5-6.5 mm long and 3.5-4.5 mm wide) which is divided in two lobes and possesses a small aperture (0.5 x 1.5 mm). The gland is located dorsally to pericardial septum of the first abdominal tergite with both lobes next to the aorta and leading to the intersegmentary membrane of the first and second tergites. De Lotto (1950) also noted two ways of discharging the liquid from the gland. The first way consists of a small secretion of the liquid that spreads through the abdomen. The second is an ejection powered by abdominal contractions, which can reach up to 8 cm. Ewer (1957) studying *Phymateus leprosus* in South Africa found three actions of the gland: i. The openings of the glands could be extruded and retracted (with no liquid expelled); ii. Extrusion of a white fluid which spreads towards the intersegmental membrane and; iii. A violent ejection of fluid that can reach up to 30 cm. Ewer (1957) also discussed two mechanisms to explain the possibility of such ejections. One is due to alary muscle contraction, and the other is due to contraction of abdomen, which increases the hemocoelic pressure.

Fishelson (1960) reported a liquid with greyish to whitish color and sharp smell in *Poekilocerus bufonius*. In adults, because of the presence of wings, the fluid spreads underneath them and when reaching the tracheal opening, the combination of air with the liquid creates bubbles of foam, which can reach up to 1.5 cm. After some minutes the foam dries and a dusty white material is left. Fishelson (1960) also reported similar glands in *Pyrgomorphella granosa* and

Pyrgomorpha conica, however, the liquid was transparent, not sticky and had a different smell compared to the plants they fed on. The liquid from *P. granosa* smelled similar to decaying meat and for *P. conica* it was close to moldy and spoilt cocoa. In the study of the Pyrgomorphidae from Madagascar, Descamps and Wintrebert (1966) reported that *Phymateus saxosus* feeds on millweed and discharges a distasteful odor. For *Rubellia nigrosignata* the odor is slightly aromatic, unpleasant but much more bearable than *P. saxosus*.

Qureshi and Ahmad (1970) studied *Poekilocerus pictus* (Pakistan) and found a difference in size and structure of the gland (fig. 1.5) and also recorded a different mechanism of discharging and behavior during disturbance. They found strong evidence that the secretion has antimicrobial properties in addition to the protection against predators. Abushama (1972) found a gland in *Poekilocerus bufonius hieroglyphicus* (Sudan) in a dorsal position with an orifice between the first and second abdominal tergites. It is located above the dorsal aorta and under the first abdominal tergite. It reaches 3-4 mm in the last instar nymphs. The gland consists of two lobes. In a stained cross section of the gland it is possible to observe to layers, the outer epithelial and the inner secretory. The secretory cells have globules which stain black-blue. Chapman et al. (1986) studied *Zonocerus variegatus* in the West and Central Africa and recorded an unpleasant smell produced by a repellent gland which opens in the dorsal midline between the first and second abdominal segments. The liquid can be ejected up to 20 cm. Some of the common names for *Z. variegatus* are “criquet puant” and “Stinkschrecke”. Its sister species, *Z. elegans,* also possesses such a gland (fig. 1.5).

Figure 1.5. Mid-dorsal abdominal gland of *Poekilocerus pictus* (India) (top) and *Zonocerus elegans* (South Africa) (bottom).

1.2.2.2 Foam emission

In the case of *Aularches miliaris* (Myanmar) fluid emission was recorded from 4 areas: i. A pair of openings on the pronotum, one on each side of the median line; ii. A pair of openings on the posterior margin of metanotum, a pair at each side of the median line; iii. A single opening on each side, close to the front coxae; iv. A single opening on each side close to the hind coxae (Hingston, 1927). In Africa, species of the genera *Taphronota* and *Dictyophorus* are well known to emit foam when disturbed (fig. 1.6). This foam is the result of ejection of haemolymph and air through abdominal spiracles and pores in the integument. Sometimes the foam can be very colorful (fig. 1.6) (COPR, 1982; Rowell et al. 2015).

Figure 1.6. *Dictyophorus griseus* emitting foam (Mozambique). **A.** Adult. **B.** Nymph. **C.** In some cases the froth could be yellow in color.

1.2.2.3 Aggregation

Nymphs of certain genera, such as *Aularches*, *Phymateus*, *Zonocerus*, *Poekilocerus* and *Taphronota,* have a tendency to form aggregations possibly to enhance protection against predators (fig. 1.7) (COPR, 1982). It has been debated whether these aggregations can be considered gregarization, which implies changes in behavior or color (Cullen et al. 2017). In some cases nymphs march in bands (fig. 1.8) and adults sometimes fly in groups (COPR, 1982; Josephrajkumar et al. 2011). For the case of *Zonocerus elegans*, they can also be found in large numbers but adults aggregate less probably due to their low mobility. Even the macropterous forms are poor flyers. Others such as *Phymateus viridipes* have shown much more sustained flight (COPR, 1982). Nymphs of *Aularches miliaris* can form bands up to 300,000 individuals, but usually they do not swarm or migrate as adults, although in some cases adults can aggregate (COPR, 1982). For *Taphronota calliparea*, it has been reported that there is a difference in color when nymphs are solitary (green) compared to when they are aggregated (black with yellow markings changing to green when molting to last instar). Adults disperse soon after (COPR, 1982).

Figure 1.7. Aggregation of nymphs of *Phymateus leprosus*.

Figure 1.8. When disturbed, *Phymateus leprosus* nymphs tend to "march" in the same direction.

1.3 Pyrgomorphidae of economic importance

1.3.1 Pest species

In 1982, The Centre for Overseas Pest Research (COPR) published *The Locust and Grasshopper Agricultural Manual*. This book, worldwide in scope, was the basis for creating the table in Appendix A. There are 62 species of Pyrgomorphidae reported to have certain degrees of economic importance (fig. 1.9). They are mainly distributed in Africa and India (COPR, 1982). The economic importance was classified from A to K as follows: A= Major pest of many crops; B= Major pest of few crops; C= Pest regularly of substantial importance (7 spp.); D= Pest occasionally of substantial importance (5 spp.); E= Pest occasionally of localized importance (11 spp.); F= A regular minor pest (3 spp.). G= An occasional minor pest (15 spp.); H= Of very minor importance at times (6 spp.); K= Few records of minor damage; negligible economic importance (12 spp.). Three species were not classified.

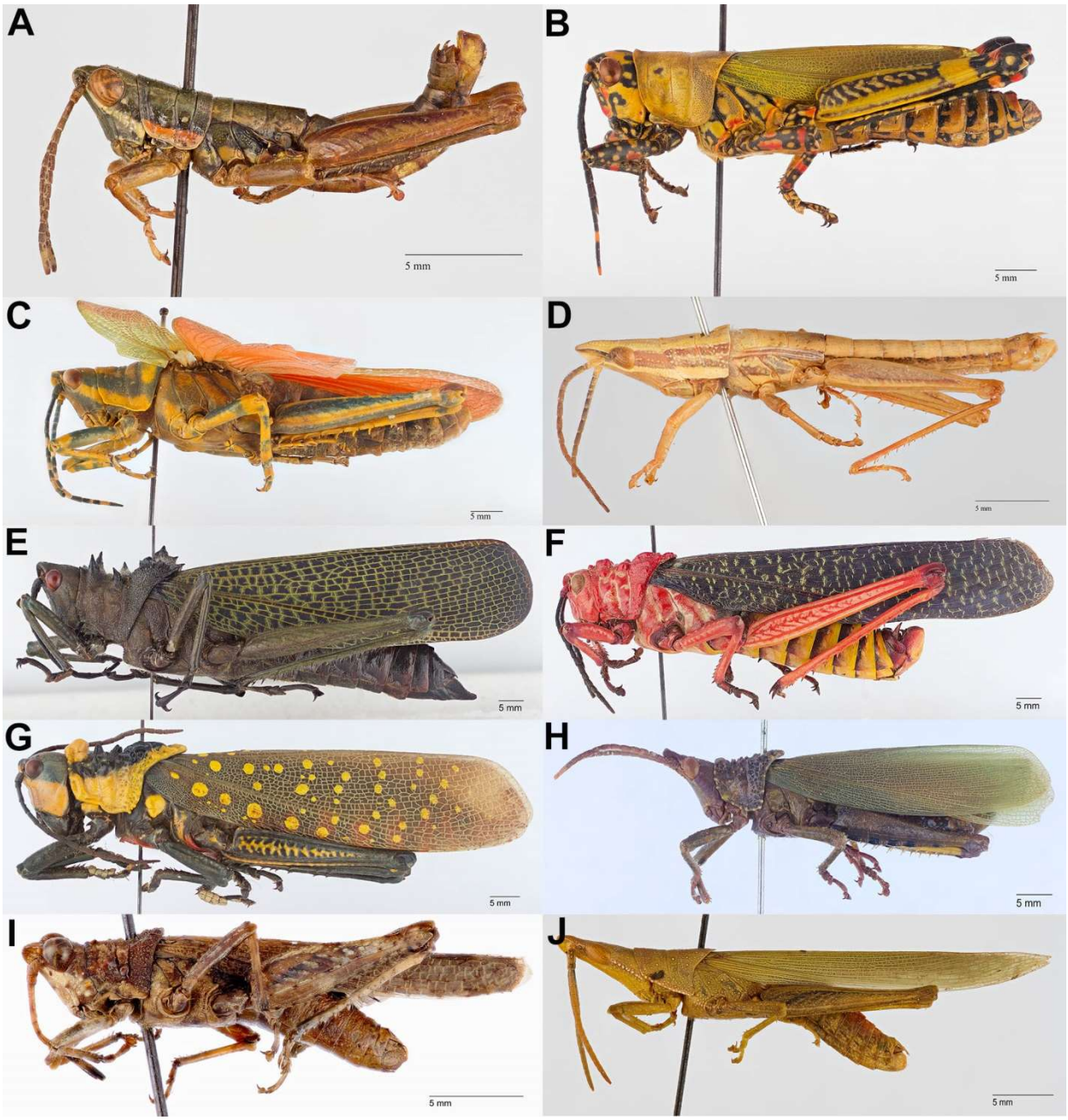

Figure 1.9. Pyrgomorphidae of economic importance. **A.** *Orthacris incongruens* (India). **B.** *Zonocerus variegatus* (Africa). **C.** *Poekilocerus pictus* (India). **D.** *Colemania sphenarioides* (India). **E.** *Rutidoderes squarrosus* (Africa). **F.** *Phymateus morbillosus* (Africa). **G.** *Aularches miliaris* (India). **H.** *Taphronota calliparea* (Africa). **I.** *Chrotogonus hemipterus* (Africa). **J.** *Atractomorpha acutipennis* (Africa).

1.3.2 Edible Pyrgomorphidae

Interestingly, while some pyrgomorphs are considered economic pests, some are used for human consumption. This is the case for *Sphenarium purpurascens* in Mexico and *Zonocerus elegans* and *Z. variegatus* in Africa.

The indigenous groups of central Mexico have consumed *Sphenarium purpurascens* from centuries (fig. 1.10A). They were known as xopanchapoli which means “summer grasshoppers” and commonly called chapulines. Its local description is as follows: “They are big and thick. They don’t fly, only crawl. They eat green beans. Some are black, others brown and others green. They are edible (Sahagún, 1577)”. A common way of preparation is to leave them one day without food or feed them with paper in order to clean the gut, boil them, sun-dry them and season with salt and lemon or garlic juice. Finally they are fried or grilled (fig. 1.10B).

Regarding *Zonocerus variegatus*, a typical recipe is to place them first in boiling water to kill them and remove head (with the gut), legs and wings. After salt is added and later they are sun-dried. Finally they are roasted, fried (could be with a mixture of spices) or boiled again. Regular consumption may be responsible for liver poisoning in humans due to the presence of pyrrolizidine alkaloids in the mid-dorsal abdominal gland (Kekeunou & Tamesse, 2016).

A synthesis of the edible Pyrgomorphidae of the world is presented in Table 1. It is based on the work of Jongema (2017) with additional references and removal of synonyms. Sub-Saharan Africa and Mexico are the places with the majority of edible pyrgomorphs (fig. 1.11).

Figure 1.10. *Sphenarium purpurascens* **A.** Nymphs and adults. **B.** Typical chapulines display in a fresh market in Oaxaca, Mexico.

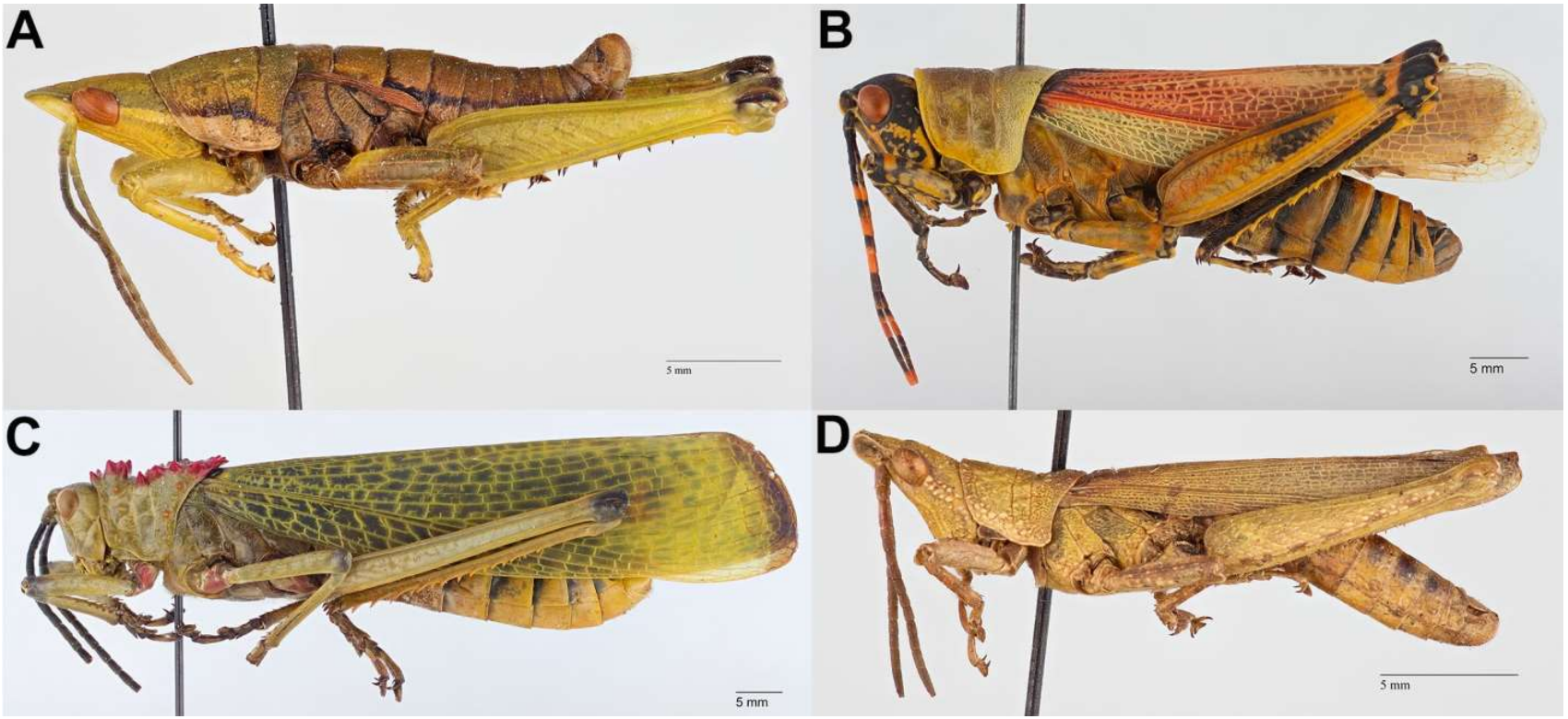

Figure 1.11. Edible Pyrgomorphidae. **A.** *Sphenarium histrio* (Mexico). **B.** *Zonocerus elegans* (Africa). **C.** *Phymateus viridipes* (Africa). **D.** *Pyrgomorpha vignaudii* (Africa).

Table 1. Edible Pyrgomorphidae of the world.

Species	Distribution	References
Chrotogonus senegalensis	Cameroon	Seignobos et al., 1996
Occidentosphena uvarovi	Congo, Gabon,	Tchibozo, 2015; Tchibozo & Lecoq, 2017
Phymateus viridipes	Congo, South Africa, Zambia, Zimbabwe, Botswana, Mozambique, Namibia	Bergier, 1941; Kelemu et al., 2015; Malaisse, 1997
Pyrgomorpha cognata	Cameroon	Barreteau, 1999
Pyrgomorpha vignaudii	Central African Republic	Hoare, 2007
Zonocerus elegans	Mozambique, South Africa. Democratic Republic of the Congo	Quin, 1959 ; Tchibozo & Lecoq, 2017
Zonocerus variegatus	Benin, Burundi, Burkina Faso, Central African Republic, Niger, Nigeria, Democratic Republic of the Congo, Cameroon, Congo, Ivory Coast, São Tomé and Príncipe, Guinea, Ghana, Togo, Liberia, Guinea Bissau, Mali, Chad, Tanzania, Sierra Leone	Barreteau, 1999; Fasoranti & Ajiboye, 1993; Kekeunou & Tamesse, 2016; Kelemu et al., 2015; Tchibozo & Lecoq, 2017
Sphenarium borrei	Mexico	Ramos-Elorduy et al., 2012
Sphenarium macrophallicum	Mexico	Pino-Moreno et al., 2016
Sphenarium histrio	Mexico	Ramos-Elorduy et al., 1998; DeFoliart, 2002
Sphenarium mexicanum	Mexico	Ramos-Elorduy & Pino-Moreno, 2002
Sphenarium purpurascens	Mexico	Ramos-Elorduy, 2006; Ramos-Elorduy et al., 1998; De Foliart, 2002; Cerritos, 2009; Cerritos & Cano-Santana, 2008
Sphenarium rugosum	Mexico	Sanabria-Urbán pers. comm.
Atractomorpha psittacina	Malaysia	Chung et al., 2002

1.4 Pyrgomorphidae conservation

Currently there are two species of Pyrgomorphidae with assessment information in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. The first one is *Pyrgomorphula serbica*, commonly known as the Serbian Stick Grasshopper. It was assessed as Critically Endangered because its extent of occurrence is only 16 km^2 in Serbia, and there are only five subpopulations with a continuing decline of mature individuals (Chobanov et al. 2016). The second species is *Pyrgomorpha cypria* (Cyprian Stick Grasshopper) (fig. 1.12). Its assessment is of Least Concern due to its widespread across the island of Cyprus (14,000 km^2). Its populations are considered stable (Willemse et al., 2016).

Josephrajkumar et al. (2011) recommended conserving *Aularches miliaris* in south India due to its local rarity, despite the fact it is very abundant and even reported as a minor agricultural pest in other parts of India. Another case is the Leichhardt's grasshopper, *Petasida ephippigera,* which is endemic to wet-dry tropics of Northern Australia. It is used for advertising Kakady and Keep River Nationals Parks. However, there are no management strategies for this emblematic pyrgomorph (Lowe, 1995). It was described in 1845 and until 1971 it was known from only five specimens (Calaby & Key, 1973). Even it is known as Aljurr, children of the lightning man among the aboriginal dreaming stories (Lowe, 1995). Due to its coloration, distribution and cultural importance, it is a good candidate to conduct an IUCN assessment and use it as a flagship species for conservation in Australia.

Five species found in Somalia are potentially endangered due to their narrow distributions. *Paraphymateus roffeyi* is known for only four or five specimens from three localities in central Somalia. *Megalopyrga monochroma* is known from the unique female holotype. *Parorthacris*

somalica is known from male material only from the type locality. *Vittisphena somalica* is known only from its type locality. *Xiphipyrgus tunstalli* has been collected only in two localities (Rowell et al., 2015). These few records could be due to the lack of recent collecting trips or due to political reasons. Nevertheless, in Kenya, which has been better explored, there is a single male specimen known for *Marsabitacris citronota* from Mount Marsabit (Rowell et al., 2015). Two species endemic to Socotra Island (part of Yemen but African in nature) are endangered due to current political issues (*Physemophorus sokotranus* and *Xenephias socotranus*). There are several other examples of pyrgomorphs known from a single or very few specimens and locality(ies). This could be due to lack of collecting or a very restricted distribution.

Figure 1.12. *Pyrgomorpha cypria*, endemic to Cyprus.

1.5 Some cultural aspects of Pyrgomorphidae

As with other familiar orthopterans, such as crickets and true locusts, Pyrgomorphidae have been recognized by different groups of people. Some of the common names reflect characteristics, such as color, defensive mechanism or damage caused to crops. For instance in India the species *Poekilocerus pictus* is known as aak or titighodo and *Aularches miliaris* as coffee locust, ghost grasshopper, Foam grasshopper, belalang setan (demon locust) (Indonesia). In Mexico *Sphenarium purpurascens* is known as xopanchapoli (summer grasshopper). In Africa, *Dictyophorus spumans* as rooibaadjie (red jacket) or Koppie foam grasshopper. *Phymateus viridipes* as green milkweed locust, *Phymateus morbillosus* as common milkweed locust. *Phymateus saxosus* as rainbow milkweed locust (Madagascar). *Zonocerus elegans* as coffee locust, elegant grasshopper, stink sprinkaan (Afrikaans) and *Zonocerus variegatus* as stink locust, variegated grasshopper, stinkschrecke, criquet puant (stinking cricket). Kekeunou & Tamesse (2016) recorded 41 different vernacular names for *Z. variegatus* from twelve countries where is distributed: adoudouba, abuzu, badenga, babbha lubhudhi, boro, babati, bakkossap, bôbô, doula doo, djaratal bahar, edja, elete, foufoumeki, fara tounfafia, fabungoundef, gozaro, gawmbo, gbata kala, hoyok mawar, jarada, kle, ma'ama, mbagsana, mêh-tseung, mahamadou ton, ou mamadi ton, ngontsoua, n'dou tooda, ngadi songo, purupuk, sagaï do, sotiété, selebongay, tata, towe, teto'dom, tsoutsounou, tangan, tonkassa, toukassa go, ukpana, vouyouk zigle hi.

In Madagascar, Braud et al. (2014) registered some vernacular names for species of *Caprorhinus* (valala seva, grasshopper of the seva shrub), *Phymateus saxosus* (valalan'alika, valalan'amboa, dog grasshopper), *Rubellia nigrosignata* (valala dingadingana, shrub grasshopper; valala tinagatinagana, valala alika-kely, small dog grasshopper; valala mahaveryzoky, grasshopper that

makes one lose his elder; valala tsybotry, wingless grasshopper; valala kitjity, small grasshopper) and *Atractomorpha acutipennis* (valala sotrobe, grasshopper with big spoon; valala tsinombina, valala tsindranolahy, grasshopper from along the river; valala sakondro, banana grasshopper; kojejan'antambo, misfortune grasshopper).

Other cultural expression is found in stamps and Pyrgomorphidae is well represented. There are representatives of Pyrgomorphidae from at least 24 countries in four continents (non-exhausting search), the African Pyrgomorphidae being the most common. In some cases, there are misidentified but in general due to their economic importance they are well identified with their common or scientific names (fig. 1.13).

Figure 1.13. Pyrgomorphidae in stamps.

CHAPTER II

SYSTEMATIC REVIEW AND TYPE INFORMATION

2.1 Taxonomic history of Pyrgomorphidae

The name Pyrgomorphidae is taken from the type genus *Pyrgomorpha,* which means πύργος, tower; μορφή, form (Audinet-Serville, 1838), possibly referring to the prominent shape of fastigium. Kevan (1964) and Kevan et al. (1969a,b) conducted a comprehensive review on the systematic history of Pyrgomorphidae and the syntheses of the nomenclatural acts are discussed below.

The earliest grouping of genera belonging to what is known as the family Pyrgomorphidae was made by Brullé (1835) who placed *Poekilocerus* Audinet-Serville 1831, *Phymateus* Thunberg 1815, *Petasia* Audinet-Serville 1831 [= *Dictyophorus* Thunberg, 1815] and *Romalea* Audinet-Serville 1831 as divisions of the subgenus *Dictyophorus* Thunberg ("les *Dictyophores*"). Of these genera, the genus *Romalea* currently belongs to another family, Romaleidae, and the others now belong to the Pyrgomorphidae. However, the name of "*Dictyophores"* was vernacular and did not meet the conditions of the International Code of Zoological Nomenclature and it cannot be argued that "Dictyophoridae" is the earliest name for the family. The publication of Kirby's (1902a) catalogue was when the first acceptable usage of a family-group name based on *Dictyophorus* became available (Dictyophorinae). Kevan and Akbar (1964) explained in detail the taxonomic history of *Dictyophorus*.

Audinet-Serville (1838) grouped *Phymateus* and *Petasia* [=*Dictyophorus*] together with some taxa that are now classified under Romaleidae and Pamphagidae in his division "Conophori". He placed *Poekilocerus* and *Truxalis* [subgenus] *Pyrgomorpha* in his division "Truxalides", and finally placed *Chrotogonus* in his subdivision "Mutici" of the division "Acridites propiè dicti". The three divisions belong to the "Famille Acridites" which is equivalent to the present superfamily Acridoidea.

Burmeister (1840) transferred *Poekilocerus* to the Conophori within which he erected the "Unterabtheilungen" Poeciloceridae (more correctly Poekiloceridae), which included two "Sektionen": Pamphagidae and Phymatidae (more correctly Phymateidae). This was the original proposal of the family-group names based on *Poekilocerus* and *Phymateus*. The name "Phymatidae" is an objective synonym of "Poeciloceridae" since the type genus of the latter was included within it. The only other included taxa, *Phymateus* and *Petasia* [=*Dictyophorus*], were regarded as "Sektionen" [subgenera] of *Poecilocera* [=*Poekilocerus*].

The oldest available name for the family known as Pyrgomorphidae is Poekiloceridae Burmeister, 1840. However, the name remained unused for the family. Scudder (1868) and Thomas (1873) both used it but only in outlining previous classificatory systems. Bolívar (1884) introduced the family-group name "Poecilocerae" for a subordinate taxon "sub-tribu". On the other hand, the name Phymat[e]idae was used by Scudder (1868), Walker (1870a,b) [Acrididae: Phymat[e]idae], Thomas (1873) [Acridinae: Phymat[e]ini], and Girard (1876).

Stål (1873) completely revised the classification of "Familia Acridiodea" (superfamily Acridoidea) and introduced a new and more extensive concept of the group ("subfamilia Phymatidae"). Brunner von Wattenwyl (1874) split Stål's Phymat[e]idea in two: "Zunft der

Pyrgomorphiden" and "Zunft der Phymat[e]iden". In 1882, Brunner von Wattenwyl (1882) latinized the name of the former group to Pyrgomorphidae. He did not deal with the group that included *Phymateus* and its relatives.

Bolívar (1884) pointed out the apparent homonymy between Phymat[e]idae (Orthoptera) and Phymatidae (Hemiptera), Bolívar ignored Brunner's divisions and followed Stål's arrangement but adopted the name Pyrgomorphidae in place of Phymat[e]idae which was soon ousted completely from the literature, except in some references. Kevan (1964) pointed out other two reasons for the general adoption of the name Pyrgomorphidae: i. Bolívar (1904, 1905 & 1909) continued to use Pyrgomorphidae; and ii. The monograph of Brunner von Wattenwyl (1882), in which the latinized form of the name was established, was the standard European work on Orthoptera for a long time. Due to the fact that there were no generally accepted rules of priority at the time, the name became firmly established in the literature. Only Yakobson & Bianchi (1902) tried to return to Phymateidae, but their work left no impression on orthopterists because it was written in Russian, and due to its rarity, it was not available to the Western authors.

For some time, the group was recognized as a tribe of the family Acrididae (Brunner von Wattenwyl, 1882; Finot, 1883; Bolívar, 1884). At first, the ending "-idae" was used (not meaning family status). Posteriorly, authors began to use the "subfamily Pyrgomorphinae" of the "family Acridiidae" or Acrididae (Bruner, 1900; Rehn, 1904, 1907). Others used the ending "-inae" but referring to the group as a tribe. However, Karsch (1891, 1893), Griffini (1897), Yakobson and Bianchi (1902, as Phymateidae), Kirby (1902a, b), Burr (1910), Bolívar (1904, 1905) treated the group as a family using the present family ending (Griffiini used "-idi") and in occasions such as Bolívar, including subfamilies within it.

Bolívar (1909) reversed his previous classification (Bolívar, 1904, 1905) and treated the group as a subfamily (Acridiidae: Pyrgomorphinae) and Kirby (1910) endorsed this action. However, Chopard (1949) later restored the family status without providing any explanation. Dirsh (1956, 1961) also recognized the group as a family. However, there was no recognition of subfamilies.

Kevan & Akbar (1964) provided a provisional arrangement of tribes, subtribes and genera. This work is complemented with the classification in two groups (A and B) proposed by Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975), which was the basis for the two subfamilies proposed by Otte (1994) that are currently in use.

Kevan (1952) initially suggested a reversal to the prior name Phymateidae, but later he retracted this idea and recommended the recognition of the name Pyrgomorphidae. Posteriorly, Kevan (1964, 1969) proposed to the International Commission on Zoological Nomenclature (ICZN) that Pyrgomorphidae, proposed as "Zunft der Pyrgomorphiden" by Brunner von Wattenwyl (1874) to be given precedence over Poekiloceridae Burmeister, 1840 and Phymateidae Burmeister, 1840. In the opinion 969 of the ICZN in 1971 the proposed changes were accepted, resulting in the family Pyrgomorphidae Brunner von Wattenwyl, 1874.

Kevan (1977) provided the most updated catalogue of the family to date. It is basically a synthesis of all his previous works with a comprehensive literature review. In its more than 600 pages, the taxonomic history of each taxon (both valid and synonym) is provided (only 62 out of the 486 valid species have been described after 1977) (fig. 2.1). This work was the basis for the catalogue of Otte (1994), which subsequently became the Orthoptera Species File online (Cigliano et al., 2018).

Bolívar and Kevan were the most prolific taxonomists for Pyrgomorphidae with 84 and 97 species descriptions, respectively (counting species described with collaborators). Bolívar was active in the late 19th century and Kevan was active in the 20th century, but they were productive for similar durations (35 and 42 years, respectively) (fig. 2.2). The first three species in the family were described by Linnaeus in 1758 (*Phymateus morbillosus, Zonocerus variegatus* and *Aularches miliaris*) and the last seven species were described by Sanabria-Urbán et al. in 2017. Other early naturalists who described some pyrgomorphids were Fabricius (6 spp.) and Thunberg (3 spp.) (Table 2.1).

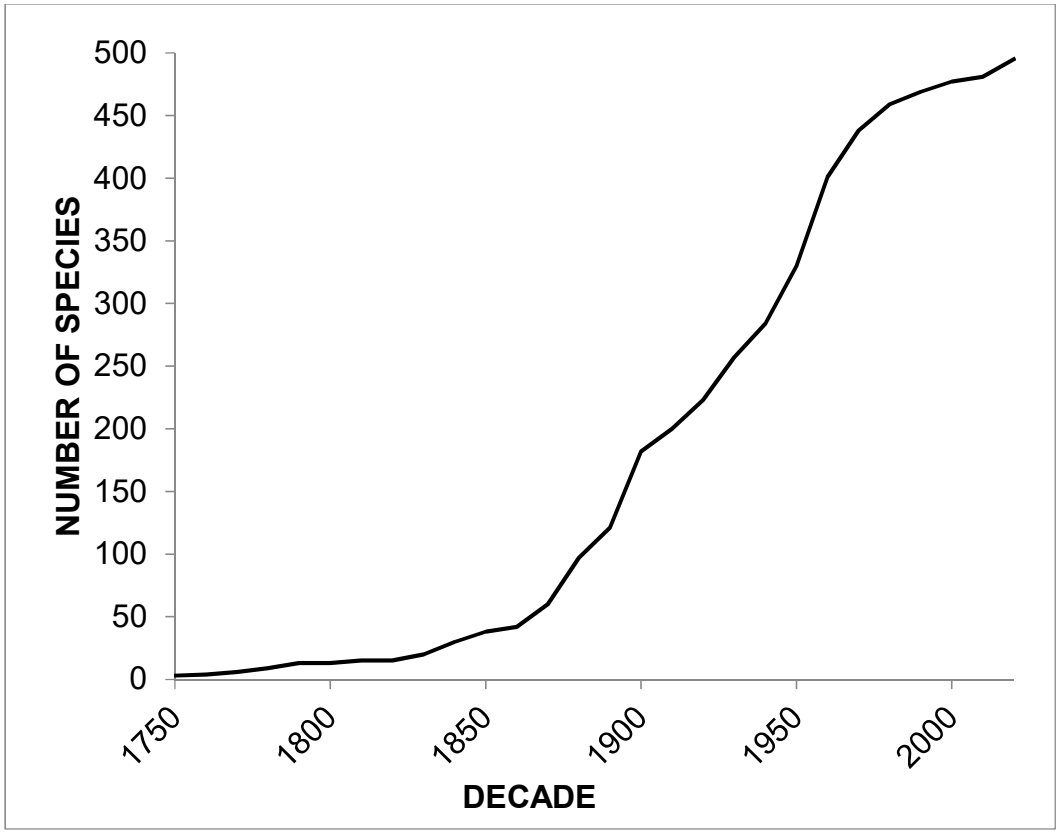

Figure 2.1. Cumulative species curve, showing the pattern of species description in Pyrgomorphidae (1758-2017).

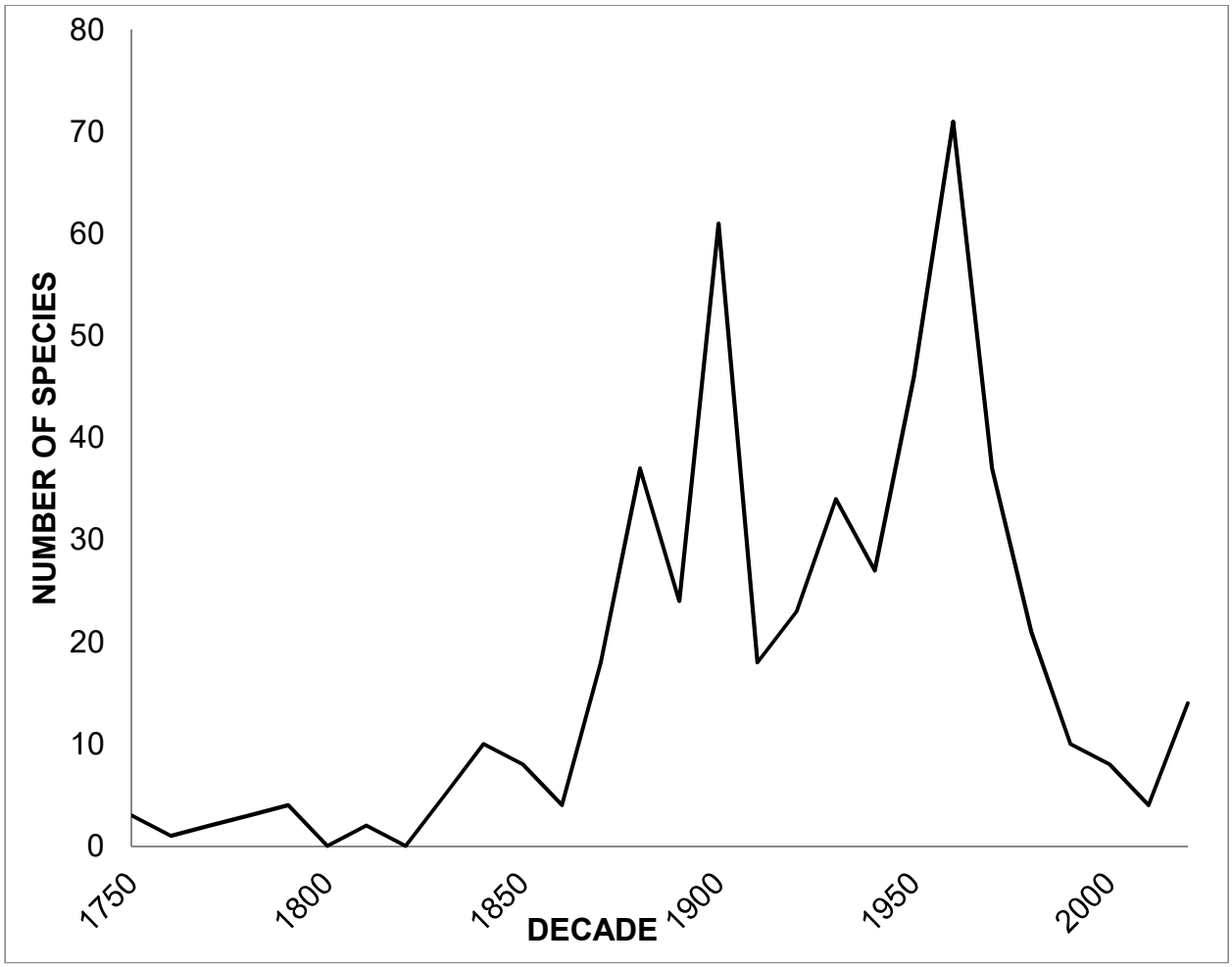

Figure 2.2. Number of species described per decade (1758-2017). The two major peaks are due to descriptions made by Bolívar and Kevan respectively.

Table 2.1. Taxonomists who described the species of Pyrgomorphidae arranged by the number of species described.

Author	Species described	Years of activity
Bolívar	84	1882-1917
Kevan	78	1948-1990
Uvarov	25	1921-1953
Wintrebert	20	1972
Karsch	19	1888-1896
Ramme	19	1929-1941
Rehn	19	1901-1953
Willemse	17	1922-1961
Dirsh	14	1951-1963
Sjöstedt	13	1910-1933
Descamps & Wintrebert	9	1966
Stål	9	1855-1877
Sanabria-Urbán, Song & Cueva del Castillo	8	2017-
Walker	8	1870-1871
Key	7	1937-1985
Blanchard	6	1836-1853
Fabricius	6	1775-1793
Kevan, Singh & Akbar	6	1964
Saussure	6	1859-1899
Brunner von Wattenwyl	5	1882-1906
Linnaeus	5	1758-1771
Bi & Xia	4	1981
Haan	4	1842
Kirby	4	1902-1914
Bruner	4	1906-1910
Bi	3	1981-1983
Carl	3	1916
Chopard	3	1921-1958
Gerstaecker	3	1869-1884
Kevan, Akbar & Singh	3	1964
Krauss	3	1877-1901
Miller	3	1934-1935
Singh & Kevan	3	1965
Thunberg	3	1787-1815
Werner	3	1908-1914
Yin	3	1984
Baccetti	2	1985
Burr	2	1898-1899
Fontana, Buzzetti, Mariño-Pérez & García García	2	2011-
Guérin-Méneville	2	1844-1849
Kevan & Akbar	2	1964
Kevan & Boyle	2	1978
Kevan & Chen	2	1969
Kevan, Akbar & Chang	2	1971
Liang	2	1988
Mao & Li	2	2015-
Perez-Gelabert, Dominici & Hierro	2	1995

Table 2.1. Continued

Author	Species described	Years of activity
Schaum	2	1853
Schmidt	2	1999-2004
Zheng	2	1992-2000
Balderson & Yin	1	1987
Charpentier	1	1842
Coquerel	1	1861
Dong & Wang	1	2012
Erichson	1	1842
Finot	1	1894
Gupta & Chandra	1	2016-
Hebard	1	1932
Hemp	1	2009-
Henry	1	1933
Huang	1	1990
Johnsen & Kevan	1	1984
Key & Kevan	1	1980
Klug	1	1832
Kuthy	1	1905
Mao & Yang	1	2003
Mao & Zheng	1	1999
Mason	1	1979
Mochulsky	1	1866
Montrouzier	1	1855
Olivier	1	1791
Reiche & Fairmaire	1	1849
Salfi	1	1939
Steinmann	1	1965
Storozhenko	1	2004
Tepper	1	1896
Wang, Xiangyu, He & Mu	1	1995
White	1	1845
Yin & Shi	1	2007
Yin, Ye & Yin	1	2009
Zheng, Huang & Zhou	1	2008
	487	

Within Pyrgomorphidae, there is a high disparity in the number of species among the 149 genera. 70 genera are monotypic, 31 genera include two species, and 17 genera include 3 species. Eight genera (*Stenoscepa, Phymateus, Orthacris, Tagasta, Parasphena, Sphenarium, Desmopterella* and *Pyrgomorpha*) comprise between 11 and 20 species and only two genera include more than twenty species (*Atractomorpha* with 27 and *Caprorhinus* with 28). This situation is due to two historical factors. First, there had been a tendency to over-split the diversity in this group, mostly by Kevan, and second, several taxa were originally described in more speciose genera but later transferred to newly erected genera.

2.2 The phylogenetic position of Pyrgomorphidae within Acridomorpha

2.2.1 Above family level

The position of Pyrgomorphidae within Acridomorpha (a monophyletic group comprising seven superfamilies; Proscopioidea, Eumastacoidea, Tanaoceroidea, Pneumoroidea, Trigonopterygoidea, Pyrgomorphoidea and Acridoidea) has not been stable until recently. In a comparative study of male phallic complex, Roberts (1941) first placed the family Pyrgomorphidae close to Pamphagidae based on the form of the ejaculatory sac and associated phallic structures, and included both families within "Chasmosacci" *sensu* Roberts (1941). This "Chasmosacci" was defined by the ejaculatory sac that runs directly into the spermatophore sac, without a major constriction associated with ventral gonopore processes on the endophallic sclerites. Also the endophallic sclerites are in ventral or medial position with respect to the spermatophore sac. Dirsh (1956) and Amédégnato (1976) placed the family close to Lentulidae based on male genitalia (endophallic simple and non-fractured sclerites). Both Dirsh and

Amédégnato placed Pyrgomorphidae within the superfamily Acridoidea. Dirsh (1975) raised "Chasmosacci" to the superfamily status as the Pamphagoidea, and Otte (1994) followed this arrangement.

The first application of modern cladistic methods in classifying Pyrgomorphidae was by Flook and Rowell (1997) who used 630 bp from mitochondrial ribosomal RNA genes of 32 caeliferan taxa (3 Pyrgomorphidae; *Prosphena scudderi*, *Atractomorpha acutipennis* and *Zonocerus elegans*) to build a phylogeny of Caelifera, but they did not recover a sister relationship between Pyrgomorphidae and Pamphagidae (fig. 2.3A).

Flook et al. (1999, 2000) using 3,177 bp from three genes (12S, 16S and 18S) did not find support for the hypothesis of a close relationship of the Pyrgomorphidae with the Lentulidae (fig. 2.3B,C) (Dirsh, 1956; Amédégnato 1976, 1993). The taxa of Pyrgomorphidae used were *Prosphena scudderi* and *Pyrgomorpha conica.* Based on this result, they proposed a new superfamily, the Pyrgomorphoidea (Flook et al., 1999). Eades (2000) hypothesized that Pyrgomorphoidea would be sister to Acridoidea based on his comparative study of male phallic complex.

Hong et al. (2003) using 480 bp from 16S rDNA from 13 taxa of Caelifera found Pyrgomorphidae (*Mekongiella kingdoni*, *Atractomorpha acutipennis* and *A. sinensis*) as a sister group of Acridoidea. They assigned *M. kingdoni* to family Chrotogonidae and both species of *Atractomorpha* to Pyrgomorphidae. Xu et al. (2003) conducted a phylogenetic analysis based on 21 morphological characters from one species of each of these 10 genera of Pyrgomorphidae (*Alaurches*, *Phymateus*, *Pseudomorphacris*, *Tagasta*, *Yunnanites*, *Mekongiella*, *Mekongiana* and *Chrotogonus, Pyrgomorpha and Atractomorpha*). They assigned the first 8 genera to the family

Chrotogonidae and the last two genera to the family Pyrgomorphidae. They concluded that both families should be merged into one family because of the lack of support for the hypothesis of two families.

Liu et al. (2005) using the male follicle morphology of 101 species of Acridoidea found relationships that are very different from what was generally accepted because they group Tetrigidae, an ancestral lineage within Caelifera, with Pyrgomorphidae (*Atractomorpha*) as a sister group to Pamphagidae and Chrotogonidae (*Aularches*, *Tagasta* and *Pseudomorphacris*).

Lu and Huang (2012) use the complete sequence of the mitochondrial COI gene of 56 species from Orthoptera. In their maximum likelihood tree, the only representative of Pneumoridae (*Physemacris variolosa*) appeared inside the Pyrgomorphidae (*Mekongiana xiangchengensis*, *Yunnanites coriacea*, *Mekongiella xizangensis*; treated as Chrotogonidae and *Atractomorpha sinensis*; treated as Pyrgomorphidae). This entire clade appeared as a sister group of the subfamily Oedipodinae in the family Acrididae (*Locusta migratoria*, *Oedalus decorus* and *Gastrimargus marmoratus*). In the Bayesian tree, the same topology appeared (Pneumoridae inside Pyrgomorphidae) but in this case, the sister group was Acridoidea, not Oedipodinae. This showed that COI gene was insufficient to resolve higher-level relationships.

Zhang et al. (2013) conducted several analyses using mithochondrial genomes and found that the concatenation of the seven NADH dehydrogenase units provided the best phylogenetic inference. In this analysis, Pyrgomorphidae (*Atractomorpha sinensis*, *Mekongiella xizangensis* and *Mekongiana xiangchengensis*) was recovered as a sister group of Acridoidea (fig. 2.3F). When using exclusively combined ribosomal dataset, Pyrgomorphidae was recovered as a sister group to Pamphagidae (4 species of Trinchinae).

Leavitt et al. (2013) using mitochondrial genome sequences of 34 species of Caelifera corroborated the relationship proposed by Eades (2000) (fig. 2.3G), but included three pyrgomorphids as part of the taxon sampling because they were the only available mitochondrial genome sequences from GenBank, all of which were from the temperate Asia (*Atractomorpha sinensis*, *Mekongiella xizangensis* and *Mekongiana xiangchengensis*). Song et al. (2015) also recovered Pyrgomorphoidea as sister to Acridoidea (fig. 2.3H) using mitochondrial genome and 4 nuclear genes (11 taxa of Pyrgomorphidae; *Atractomorpha*, *Mekongiella*, *Mekongiana*, *Chrotogonus*, *Pyrgormorpha*, *Monistria*, *Desmoptera*, *Algete*, *Colemania* and *Phymateus*).

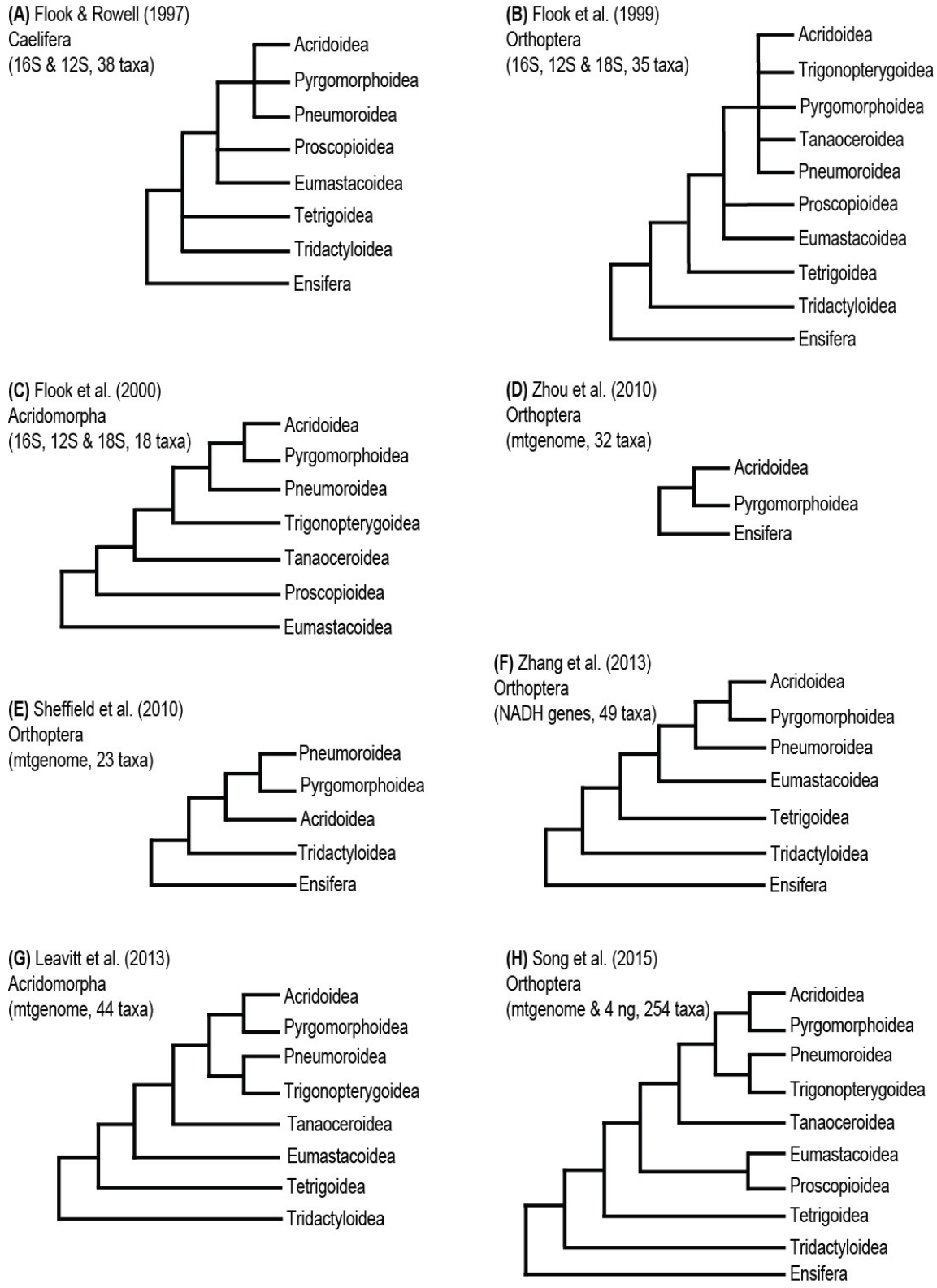

Figure 2.3. Previous phylogenetic hypotheses of Orthoptera based on modern phylogenetic methods that included Pyrgomorphidae, the sole member of superfamily Pyrgomorphoidea.

2.2.2 Below family level

There is strong evidence that the family Pyrgomorphidae is a monophyletic group. Externally the presence of a groove in the fastigium (Kevan & Akbar 1964) coupled with very distinctive internal male genitalic structures such as the cingulum extending around to the ventral side, the endophallic apodemes turned medially, and the ejaculatory sac opening to the genital chamber are the characteristics defining the family, which are present in all of the described taxa (Eades & Kevan, 1974; Eades, 2000). In recent molecular studies (Zhang et al., 2013; Leavitt et al., 2013; Song et al., 2015) as well as a morphological phylogenetic analysis (Mariño-Pérez and Song 2018), Pyrgomorphidae was recovered as monophyletic with strong nodal support values.

In 1968, Descamps (1968) described a highly unusual monotypic genus from the island of Mauritius in the Indian Ocean and named *Pyrgacris* because it had somewhat intermediate characters between Pyrgomorphidae and Acrididae. While examining the phallic musculature of Pyrgomorphidae, Eades and Kevan (1974) examined *Pyrgacris*, and determined that it would belong to Pyrgomorphidae and established a new subfamily Pyrgacrinae, noting its similarities with Acrididae. Later, Pyracridinae was included as a subfamily of Pyrgomorphidae in the works of Dirsh (1975), Kevan (1977, 1982), Otte (1994), and Vickery (1997).

Dirsh (1975) published a controversial classification of Acridomorpha in which he created many subfamilies and families, which were not generally adopted by other authors. In this work, he divided Pyrgomorphidae into 13 subfamilies (Atractomorphinae, Chrotogoninae, Desmopterinae, Dictyophorinae, Fijipyrginae, Geloiinae, Nereniinae, Omurinae, Phymateinae, Psednurinae, Pyrgacrinae, Pyrgomorphinae and Zonocerinae), which partially overlapped with Kevan's (1969, 1970, 1971, 1972, 1974, 1975) proposal but left behind several genera. Dirsh (1975) indicated

that his classification of Pyrgomorphidae was based mostly based on external characteristics because he argued that grouping on the basis of internal genitalia was particularly difficult for this group because of the diversity in the epiphallus and ectophallus in almost every genus. This classification was followed by Mason (1979), but not by others.

In his monumental catalogue of Pyrgomorphidae, Kevan (1977) divided the family into two subfamilies, Pyrgacridinae and Pyrgomorphinae, the latter following the previous classification of the same author (Kevan et al., 1969, 1970, 1971, 1972, 1974, 1975) of the groups A and B.

Chinese authors have followed a different classification scheme, and Yin (1982, 1984) placed pyrgomorphs within Acridoidea and divided it into two families with vague characters with multiple exceptions: Chrotogonidae, with four subfamilies (Taphronotinae, Chrotogoninae, Yunnanitinae and Mekongiellinae) and Pyrgormophidae, with two subfamilies (Pyrgormorphinae and Atractomorphinae). Xia et al. (1994) followed Yin's scheme and added two more subfamilies (Aularchinae and Tagastinae) to Chrotogonidae.

In publication of the paper version of the Orthoptera Species File, Otte (1994) divided the family into three subfamilies: Pyrgacrinae (to accommodate the genus *Pyrgacris*), Orthacridinae (erected by Bolívar in 1905), and Pyrgomorphinae (type subfamily). The latter two corresponded to the groups A and B of Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975). Also, the recently created tribe Petasidini (Key, 1985 transferred the genera *Petasida* and *Scutyllia* from Monistrini) was included in the subfamily Pyrgomorphinae.

Vickery (1997) basically followed Otte (1994) and divided the family Pyrgomorphidae into three subfamilies: Pyrgacridinae, Orthacridinae, and Pyrgomorphinae. The latter two subfamilies

basically followed Kevan's group A and B, respectively. The only difference was the addition of the tribe Petasidini to the subfamily Pyrgomorphinae.

Eades (2000) performed a comparative study of the phallic complex across Acridomorpha and discussed that there was enough evidence to elevate the subfamily Pyrgacridinae to a family level. Also, due to the differences in internal genitalia, which resemble Acridoidea more than Pyrgomorphoidea, and he decided to place the family Pyrgacrididae in the superfamily Acridoidea. Since then, the Orthoptera Species File online (Cigliano et al., 2018) has maintained the family Pyrgomorphidae divided into two subfamilies, Orthacridinae (15 tribes) and Pyrgomorphinae (16 tribes), while treating Pyrgacrididae as a separate family (Table 2.2).

Table 2.2. Tribes for each subfamily of Pyrgomorphidae. (taken from Orthoptera Species File) with their corresponding Group and Series (Kevan, 1976, Kevan et al., 1969, 1970, 1971, 1972, 1974, 1975)

Subfamily Orthacridinae	Kevan Group and Series	Subfamily Pyrgomorphinae**	Kevan Group and Series
Fijipyrgini Kevan, 1966	A/I	Desmopterini Bolívar, 1905	B/V
Verduliini Kevan & Akbar, 1964	A/I	Monistrini Kevan & Akbar, 1964	B/V
Brunniellini Kevan, 1963	A/I	Petasidini Key, 1985	B/V*
Psednurini Burr, 1904	A/I	Chlorizeinini Kevan & Akbar, 1964	B/VI
Mitricephalini Kevan & Akbar, 1964	A/I	Poekilocerini Burmeister, 1840	B/VI
Geloiini Bolívar, 1905	A/II	Phymateini Bolívar, 1884	B/VI
Sagittacridini Descamps & Wintrebert, 1966	A/II	Schulthessiini Kevan & Akbar, 1964	B/VII
Gymnohippini Kevan & Akbar, 1964	A/II	Taphronotini Bolívar, 1904**	B/VII
Malagasphenini Kevan & Akbar, 1964	A/II	Dictyophorini Kirby, 1902	B/VII
Chapmanacridini Kevan & Akbar, 1964	A/III	Tagastini Bolívar, 1905	B/VIII
Ichthiacridini Kevan, Singh & Akbar, 1964	A/III	Pseudomorphacridini Kevan & Akbar, 1964	B/VIII
Ichthyotettigini Kevan, Singh & Akbar, 1964	A/III	Atractomorphini Bolívar, 1905	B/VIII
Orthacridini Bolívar, 1905**	A/III	Sphenariini Bolívar, 1884	B/IX
Popoviini Kevan & Akbar, 1964	A/III	Omurini Kevan 1961	B/IX
Nereniini Kevan 1964	A/IV	Pyrgomorphini Brunner von Wattenwyl, 1882**	B/X
		Chrotogonini Bolívar, 1904	B/X

*Petasidini was included by Kevan (1974) in Monistrini, Key (1985) elevated to tribe level and Otte (1994) assigned to subfamily Pyrgomorphinae.

Due to external morphological resemblance, some taxa of other families were initially classified as Pyrgomorphidae. As time passed, the family was better defined and some taxa were removed and transferred to different families. An account of the previous taxa once considered Pyrgomorphidae is given in Table 2.3.

Table 2.3. Taxa removed from Pyrgomorphidae.

Family	Genera
Trigonopterygidae	*Borneacris, Trigonopteryx, Systella, Moultonia*
Xyronotidae	*Xyronotus*
Pyrgacrididae	*Pyrgacris*
Pamphagodidae	*Charilaus, Pamphagodes*
Ommexechidae	*Graea, Ommexecha, Clarazella*
Romaleidae	*Dracotettix, Legua*
Acrididae	*Aspidophyma*

2.2.3 Only known fossil

Heer (1865) reported a grasshopper fossil from Oeningen, Germany. It was dated to be from the Upper Miocene (11.6 to 5.3 mya). Originally it was named *Oedipoda fischeri* and posteriorly Scudder (1891) transferred it to the genus *Chimarocephala*. Zeuner (1944) discussed its affinities with the genus *Pyrgomorpha* with differences in the tegmina length and width and hind femur shape. Kevan & Akbar (1964) placed it in a new genus *Miopyrgomorpha* (fig. 2.4) but it was only a hundred years after its original description that Kevan (1965) properly described it as follows: "Similar to *Pyrgomorpha* Audinet-Serville, 1838 (fig. 2.5), but vertex less convex and frons less concave in lateral view. Tegmina broader and more rounded at apex. Hind femur stouter, shorter that abdomen and shorter than hind tibia." Kevan (1965) also discussed its affinities to the only two other European Pyrgomorphidae, *Pyrgomorpha conica* and *Pyrgomorphula serbica*. However, he stated that its closest living relative appears to be *Pyrgomorphula turcica* (Nowadays synonym of *Pyrgomorpha guentheri*) from southeast Turkey.

Figure 2.4. *Miopyrgomorpha fischeri* Upper Miocene (11.6 to 5.3 mya) Eidgenössische Technische Hochschule, Zürich, Switzerland.

Figure 2.5. The species *Pyrgomorpha vignaudii* belongs to the closest living genera hypothesized to be a relative of the only known pyrgomorph fossil *Miopyrgomorpha fischeri*.

2.3 Type information

2.3.1 List of type species information

The type depository and country of type locality to generate the table of this section was gathered from three different sources. The catalogue of Kevan (1977), the Orthoptera Species File (Cigliano et al., 2018) (based on the catalogue of Otte, 1993), and visits to museums conducted during 2013-2017. Personally, I visited fourteen museums in eleven countries to take images of type material (56 days in six different trips). I was able to request two colleagues (Hojun Song and Bert Foquet) to obtain images in other 6 museums in three countries. All the images of type material were uploaded to Orthoptera Species File and, in several occasions, type material of synonyms was also photographed. As a result of this project, there is an increase from 121 to 421 (out of 548) of the species and subspecies with photographic record. This increase from 22 to 77% has positioned the family Pyrgomorphidae as one of the most well-digitized orthopteran groups represented at OSF. As an example here is a link to OSF.

http://orthoptera.speciesfile.org/Common/basic/ShowImage.aspx?TaxonNameID=1121201&ImageID=224386

Table 2.4. Type species information. HT=Holotype, AT=Allotype, PT= Paratype, LT=Lectotype, PLT=Paralectotype, ST, Syntype, NT= Neotype, NAT=Neoallotype, T=Type. Specimen in **BOLD** were photographed as part of this dissertation. Images of specimens shaded in grey were already available from other sources. For Museum depository see footnote.

Species or subspecies	Types	Type locality
Acanthopyrgus finoti (Bolívar, 1905)	**LT ♂ MNHN; PLT ♂ MNHN; PLT ♂ MNCN**	MADAGASCAR
Acanthopyrgus longicornis Descamps & Wintrebert, 1966	**HT ♂ MNHN**	MADAGASCAR
Acropyrgus cadeti Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN; PT ♂ MNCN**	MADAGASCAR
Afrosphenella capensis (Key, 1937)	**HT ♂ BMNH; AT ♀ BMNH**	SOUTH AFRICA
Afrosphenella senecionicola (Key, 1937)	**HT ♂ BMNH; AT ♀ BMNH**	SOUTH AFRICA
Algete brunneri Bolívar, 1905	**HT ♀ NMW**	BRAZIL
Ambositracris morati Kevan, Akbar & Chang, 1971	**HT ♀ MNHN**	MADAGASCAR
Ambositracris ornata Dirsh, 1963	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Ambositracris vittata (Kevan, Akbar & Singh, 1964)	**HT ♂ ANSP; AT ♀ ANSP**	MADAGASCAR
Anarchita aptera (Bolívar, 1902)	**LT ♂ MNCN; PLT ♀ MNCN**	INDIA
Annandalea haematoptera (Haan, 1842)	**ST ♂ NBC; ST ♀ NBC**	INDONESIA
Annandalea robinsoni Bolívar, 1905	**HT ♂ MNCN**	MALAYSIA
Apodesmoptera (*Apodesmoptera*) *curtipennis* Kevan, 1966	HT ♂ BPBM	PHILIPPINES
Apodesmoptera (*Apodesmoptera*) *mira* Rehn, 1951	**HT ♂ ANSP; AT ♀ ANSP**	PHILIPPINES
Apodesmoptera (*Brachydesmoptera*) *luzonica* Kevan, 1963	**HT ♀ ANSP**	PHILIPPINES
Arbuscula cambodjiana Bolívar, 1905	**HT ♀ MNCN**	CAMBODIA
Atractomorpha aberrans Karsch, 1888	**HT ♀ MfN**	ANGOLA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Atractomorpha acutipennis acutipennis (Guérin-Méneville, 1844)	**HT ♂ MHNG**	MADAGASCAR
Atractomorpha acutipennis blanchardi Bolívar, 1905	NT ♀ USNM	INDIA
Atractomorpha acutipennis brevis Uvarov, 1938	**HT ♂ EFC**	YEMEN
Atractomorpha acutipennis gerstaeckeri Bolívar, 1884	**LT ♀ MNCN; PLT ♂ MNCN**	GABON
Atractomorpha angusta Karsch, 1888	**LT ♂ MfN**	INDONESIA
Atractomorpha australis Rehn, 1907	HT ♀ AMNH	AUSTRALIA
Atractomorpha burri Bolívar, 1905	**LT ♀ MNCN; PLT ♂ MNCN**	INDIA
Atractomorpha crenaticeps (Blanchard, 1853)	**LT ♀ MNCN; PLT ♂ MNCN; PLT ♂ MNHN**	PAPUA NEW GUINEA
Atractomorpha crenulata crenulata (Fabricius, 1793)	**ST ♀ ZMUC; ST ♀ ZMUC**	INDIA
Atractomorpha crenulata prasina Bolívar, 1905	**LT ♂ MNCN; PLT ♂ MNCN**	INDIA ?
Atractomorpha dubia Wang, Xiangyu, He & Mu, 1995	Shandong	CHINA
Atractomorpha fuscipennis Liang, 1988	HT ♂ ICRI	CHINA
Atractomorpha himalayica Bolívar, 1905	**HT ♀ MNCN**	INDIA
Atractomorpha hypoestes Key & Kevan, 1980	**HT ♂ ANIC**	AUSTRALIA
Atractomorpha lata (Mochulsky, 1866)	ST ♂ ZMUM; ST ♀ ZMUM	JAPAN
Atractomorpha melanostriga Bi, 1981	IZCAS	CHINA
Atractomorpha micropenna Zheng, 1992	???	CHINA
Atractomorpha nigripennis Zheng, 2000	Shaanxi	CHINA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Atractomorpha occidentalis Kevan & Chen, 1969	HT ♂ LEMQ; **PT ♂ MNHN; PT ♀ MNHN**	LIBERIA
Atractomorpha orientalis Kevan & Chen, 1969	HT ♂ LEMQ; **PT ♂ MfN**	DEMOCRATIC REPUBLIC OF THE CONGO
Atractomorpha peregrina Bi & Xia, 1981	HT ♂ IEAS	CHINA
Atractomorpha psittacina affinis Kevan & Chen, 1969	HT ♂ LEMQ	INDIA
Atractomorpha psittacina psittacina (Haan, 1842)	**LT ♂ NBC**	MALAYSIA/INDONESIA
Atractomorpha rhodoptera Karsch, 1888	**HT ♀ MfN**	INDONESIA
Atractomorpha rufopunctata Bolívar, 1894	**LT ♀ MNCN**	TOGO
Atractomorpha sagittaris Bi & Xia, 1981	HT ♂ IEAS	CHINA
Atractomorpha similis Bolívar, 1884	**LT ♂ ISNB; PLT ♂ ISNB; PLT ♀ ISNB**	INDONESIA
Atractomorpha sinensis montana Kevan & Chen, 1969	HT ♂ LEMQ	INDIA
Atractomorpha sinensis sinensis Bolívar, 1905	**HT ♀ MNHN**	CHINA
Atractomorpha suzhouensis Bi & Xia, 1981	HT ♂ IEAS	CHINA
Atractomorpha taiwanensis Yin & Shi, 2007	HT ♂ MHU	TAIWAN
Atractomorpha yunnanensis Bi & Xia, 1981	HT ♂ IEAS	CHINA
Aularches miliaris miliaris (Linnaeus, 1758)	LT ♂ LSUK	INDIA
Aularches miliaris pseudopunctatus Kevan, 1974	HT ♂ LEMQ	INDIA
Brunniella antistes Bolívar, 1905	HT ♀ ZMUH	PHILIPPINES

Table 2.4. Continued

Species or subspecies	Types	Type locality
Buergersius olivaceus Ramme, 1930	**HT ♂ MfN; PT ♂ MfN**	PAPUA NEW GUINEA
Burmorthacris aptera Kevan, Singh & Akbar, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MYANMAR
Buyssoniella madecassa Bolívar, 1905	HT ♀ LOST	MADAGASCAR
Caconda burri Kevan, 1952	**HT ♀ BMNH**	ANGOLA
Caconda fusca Bolívar, 1884	**HT ♀ MNCN**	ANGOLA
Calamacris clendoni Rehn, 1904	**LT ♂ ANSP; PLT ♀ ANSP**	MEXICO
Camoensia insignis insignis Bolívar, 1882	**PLT ♂ MNCN; PLT ♀ MNCN**	ANGOLA
Camoensia insignis sculpturata Bolívar, 1904	**HT ♂ MNCN**	WEST AFRICA
Caprorhinus ambahitae Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus andohahalensis Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus anivoranensis Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus betrokae Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus cadeti Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus dechappei Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus descampsi Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus donskoffi Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus fotadrevensis Kevan, Akbar & Chang, 1971	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus fusiformis Saussure, 1899	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus inflatus Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR

Table 2.4. Continued

Species or subspecies	Types	Type locality
Caprorhinus isoanalae Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus kevani Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus lavanonensis Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus mahabensis Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus major Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus malzyi Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus minor Uvarov, 1929	**HT ♂ BMNH**	MADAGASCAR
Caprorhinus monclari Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus pauliani Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus puerisalbis Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus ralinoroi Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus ranohirae Kevan, 1963	HT ♂ CAS	MADAGASCAR
Caprorhinus rostratus Uvarov, 1929	**HT ♂ BMNH**	MADAGASCAR
Caprorhinus seyrigi Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Caprorhinus squamipennis Bruner, 1910	**LT ♂ MfN; PLT ♀ MfN**	MADAGASCAR
Caprorhinus tenikae Wintrebert, 1972	**HT ♂ MNHN**	MADAGASCAR
Caprorhinus zolotarevskyi Uvarov, 1929	**HT ♂ BMNH; PT ♀ BMNH**	MADAGASCAR
Carinisphena producta Kevan, 1966	HT ♀ TMSA	SOUTH AFRICA
Cawendia glabrata Karsch, 1888	**LT ♀ MfN; PLT ♂ MfN**	TANZANIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Chapmanacris sylvatica Dirsh, 1959	**HT ♂ BMNH**	GHANA
Chirindites odendaali Ramme, 1929	**HT ♂ BMNH; PT ♀ BMNH**	ZIMBABWE
Chlorizeina feae Kevan, 1969	HT ♂ USNM	THAILAND
Chlorizeina togulata Rehn, 1951	**HT ♂ ANSP; AT ♀ ANSP**	MYANMAR
Chlorizeina unicolor roonwali Bhowmik, 1964	HT ♀ NZSI	INDIA
Chlorizeina unicolor unicolor Brunner von Wattenwyl, 1893	**ST ♀ MHNG**	MYANMAR
Chlorizeina yunnana Mao & Li, 2015	HT ♂ BMDU	CHINA
Chrotogonus (*Chrotogonus*) *armatus* Steinmann, 1965	HT ♀ HNHM	CHINA
Chrotogonus (*Chrotogonus*) *brachypterus* Bolívar, 1902	**LT ♂ MNCN**	INDIA
Chrotogonus (*Chrotogonus*) *hemipterus* Schaum, 1853	**LT ♂ MfN; PLT ♀ MfN**	MOZAMBIQUE
Chrotogonus (*Chrotogonus*) *homalodemus homalodemus* (Blanchard, 1836)	**HT ♀ MNHN**	SUDAN
Chrotogonus (*Chrotogonus*) *homalodemus somalicus* Kevan, 1959	HT ♀ BMNH	SOMALIA
Chrotogonus (*Chrotogonus*) *oxypterus* (Blanchard, 1836)	**ST ♀ MNHN; ST ♀ MNHN**	INDIA
Chrotogonus (*Chrotogonus*) *senegalensis abyssinicus* Bolívar, 1904	**HT ♂ MNHN**	ETHIOPIA
Chrotogonus (*Chrotogonus*) *senegalensis brevipennis* Kevan, 1959	HT ♀ BMNH**; 3PT ♀ MNHN; 2 PT ♂ MNHN; PT ♀ MfN; PT ♂ MfN**	SUDAN?
Chrotogonus (*Chrotogonus*) *senegalensis gabonicus* Bolívar, 1904	HT ♀ MNHN	ANGOLA
Chrotogonus (*Chrotogonus*) *senegalensis senegalensis* Krauss, 1877	**HT ♀ NMW**	SENEGAL

Table 2.4. Continued

Species or subspecies	Types	Type locality
Chrotogonus (*Chrotogonus*) *senegalensis sudanicus* Kevan, 1959	**HT ♀ MNHN; AT ♂ MNHN**	SUDAN
Chrotogonus (*Chrotogonus*) *trachypterus robertsi* Kirby, 1914	ST ♀ BMNH	PAKISTAN
Chrotogonus (*Chrotogonus*) *trachypterus trachypterus* (Blanchard, 1836)	**ST ♀ MNHN; ST ♀ MNHN**	INDIA
Chrotogonus (*Chrotogonus*) *turanicus* Kuthy, 1905	NT ♂ MNCN	KAZAKHSTAN
Chrotogonus (*Obbiacris*) *arenicola* Kevan, 1952	**HT ♂ ETHZ; PT ♀ ETHZ**	SOMALIA
Chrotogonus (*Obbiacris*) *tuberculatus* Kevan, 1959	**HT ♀ BMNH; AT ♂ BMNH**	KENYA
Colemania sphenarioides Bolívar, 1910	**LT ♂ MNCN; PLT ♀ MNCN**	INDIA
Desmoptera (*Desmoptera*) *analis* Ramme, 1941	HT ♂ Stettin**; PT ♂ MfN**	INDONESIA
Desmoptera (*Desmoptera*) *irianica* Kevan, 1982	HT ♀ NBC	PAPUA NEW GUINEA
Desmoptera (*Desmoptera*) *judicata* Bolívar, 1884	HT ♀ BMNH**; AT ♂ MfN**	INDONESIA
Desmoptera (*Desmoptera*) *novaeguineae* (Haan, 1842)	**LT ♀ NBC**	INDONESIA
Desmoptera (*Desmoptera*) *truncatipennis* Sjöstedt, 1920	**HT ♂ NHRS**	AUSTRALIA
Desmoptera (*Desmopterula*) *degenerata degenerata* Brunner von Wattenwyl, 1898	**ST ♂ NMW**	INDONESIA
Desmoptera (*Desmopterula*) *degenerata molucensis* Bolívar, 1905	**LT ♂ MNCN; PLT ♀ MNCN**	INDONESIA
Desmopterella angustata Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	PAPUA NEW GUINEA
Desmopterella biroi (Bolívar, 1905)	**LT ♀ NHRS; PLT ♀ MNCN**	PAPUA NEW GUINEA
Desmopterella buergersi Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	PAPUA NEW GUINEA
Desmopterella cercata Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	PAPUA NEW GUINEA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Desmopterella circe Kevan, 1970	HT ♂ ANIC	PAPUA NEW GUINEA
Desmopterella curvata Kevan, 1970	HT ♂ BPBM	INDONESIA
Desmopterella curvicercis Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	PAPUA NEW GUINEA
Desmopterella dahli Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	PAPUA NEW GUINEA
Desmopterella denticulata Ramme, 1941	**HT ♂ MfN; AT ♀ MfN**	INDONESIA
Desmopterella esme Kevan, 1970	**HT ♂ NBC; AT ♀ NBC**	INDONESIA
Desmopterella explicata (Karsch, 1888)	**HT ♀ MfN**	PAPUA NEW GUINEA
Desmopterella haani (Bolívar, 1898)	**LT ♂ MCSN; PLT ♂ MNCN; PLT ♀ MNCN**	PAPUA NEW GUINEA
Desmopterella keyensis Kevan, 1970	HT ♂ BMNH	INDONESIA
Desmopterella marginata (Bolívar, 1898)	**LT ♀ MCSN; PLT ♀ MNCN**	PAPUA NEW GUINEA
Desmopterella prasina (Bolívar, 1905)	NT ♀ BMNH	PAPUA NEW GUINEA
Desmopterella sundaica steini Ramme, 1941	HT ♂ MfN	PAPUA NEW GUINEA
Desmopterella sundaica sundaica (Rehn, 1909)	HT ♀ AMNH	INDONESIA
Desmopterella sylvatica (Montrouzier, 1855)	NT ♀ BPBM	PAPUA NEW GUINEA
Desmopterella willemsei Kevan, 1970	HT ♂ CAS	INDONESIA
Dictyophorus (*Dictyophorus*) *cuisinieri* (Carl, 1916)	**HT ♀ MHNG**	GUINEA
Dictyophorus (*Dictyophorus*) *spumans ater* (Distant, 1892)	HT ♂ BMNH	SOUTH AFRICA
Dictyophorus (*Dictyophorus*) *spumans calceata* (Bolívar, 1904)	**HT ♀ MNCN**	NAMIBIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Dictyophorus (*Dictyophorus*) *spumans pulchra* (Bolívar, 1904)	HT ♂ ZMUH	SOUTH AFRICA
Dictyophorus (*Dictyophorus*) *spumans servillei* (Bolívar, 1904)	LT ♂ MNCN	SOUTH AFRICA
Dictyophorus (*Dictyophorus*) *spumans spumans* (Thunberg, 1787)	**LT ♂ UZIU; 2 PLT ♂ UZIU**	SOUTH AFRICA
Dictyophorus (*Tapesiella*) *griseus griseus* (Reiche & Fairmaire, 1849)	**LT ♂ MNHN**	ETHIOPIA
Dictyophorus (*Tapesiella*) *griseus oberthueri* (Bolívar, 1894)	**HT ♀ MNCN; PT ♀ MNCN**	TOGO
Dictyophorus (*Tapesiella*) *karschi* (Bolívar, 1904)	**LT ♂ ISNB; PLT ♀ ISNB**	DEMOCRATIC REPUBLIC OF THE CONGO
Doriaella cheesmanae Kevan, 1966	**HT ♀ BMNH**	PAPUA NEW GUINEA
Doriaella cinnabarina Bolívar, 1898	**HT ♂ MCSN**	PAPUA NEW GUINEA
Dyscolorhinus squalinus Saussure, 1899	**LT ♀ MHNG**	MADAGASCAR
Dyscolorhinus vittatus Kevan, Akbar & Singh, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MADAGASCAR
Eilenbergia sagitta Mason, 1979	**PT ♂ BMNH**	ANGOLA
Feacris malabarensis (Kevan, 1953)	HT ♂ USNM	INDIA
Feacris reducta Kevan, 1969	HT ♀ LEMQ	INDIA
Fijipyrgus gracilis Kevan, 1966	HT ♂ BPBM	FIJI
Fusiacris spinata Willemse, 1955	**HT ♀ NBC; PT ♂ NBC**	INDONESIA
Fusiacris uniformis Willemse, 1955	HT ♀ NHME; **PT ♀ NHME**	INDONESIA
Geloiodes cavifrons Chopard, 1958	**HT ♀ MNHN**	SÃO TOMÉ AND PRÍNCIPE
Geloius crassicornis Bolívar, 1905	**HT ♀ MNHN**	MADAGASCAR

Table 2.4. Continued

Species or subspecies	Types	Type locality
Geloius nasutus Saussure, 1899	**LT ♀ MNHG; NAT ♂ MNHN; PLT ♀ MNHN**	MADAGASCAR
Geloius tanalanensis Wintrebert, 1972	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Greyacris picta (Sjöstedt, 1921)	**LT ♀ MNCN**	AUSTRALIA
Greyacris profundesulcata (Carl, 1916)	**HT ♀ MHNG**	AUSTRALIA
Gymnohippus marmoratus Bruner, 1910	**LT ♀ MfN**	MADAGASCAR
Humpatella constricta Karsch, 1896	**HT ♂ MfN**	ANGOLA
Humpatella huambae Uvarov, 1953	HT ♂ BMNH	ANGOLA
Humpatella nigropicta (Bolívar, 1889)	HT ♀ LZLP LOST	ANGOLA
Humpatella severini Bolívar, 1904	**ST ♀ ISNB**	DEMOCRATIC REPUBLIC OF THE CONGO
Ichthiacris (*Atyphacris*) *aptera* Hebard, 1932	**LT ♂ ANSP; PLT ♀ ANSP**	MEXICO
Ichthiacris (*Atyphacris*) *californica* Bolívar, 1905	**LT ♂ MNHN**	MEXICO
Ichthiacris (*Atyphacris*) *celata* Kevan, 1990	HT ♂ CAS	MEXICO
Ichthiacris (*Atyphacris*) *costulata* Bolívar, 1905	**HT ♀ MNHN**	MEXICO
Ichthiacris (*Atyphacris*) *elongata* Kevan, Singh & Akbar, 1964	HT ♂ CAS	MEXICO
Ichthiacris (*Ichthiacris*) *parva* Kevan, 1990	HT ♂ CAS	MEXICO
Ichthiacris (*Ichthiacris*) *rehni* Bolívar, 1905	**LT ♂ MNHN; PLT ♀ MNHN; PLT ♂ MNCN; PLT ♀ MNCN**	MEXICO
Ichthiacris (*Ichthiacris*) *spinifera* Kevan, 1990	HT ♂ CAS	MEXICO

Table 2.4. Continued

Species or subspecies	Types	Type locality
Ichthyotettix inexpectatus Fontana, Buzzetti, Mariño-Pérez & García García, 2011	HT ♂ UNAM	MEXICO
Ichthyotettix mexicanus (Saussure, 1859)	**LT ♂ MHNG; PLT ♀ MHNG**	MEXICO
Ichthyotettix stricticaudatus Fontana, Buzzetti, Mariño-Pérez & García García, 2011	HT ♂ UNAM	MEXICO
Jaragua oviedensis Perez-Gelabert, Dominici & Hierro, 1995	HT ♂ ANSP; **PT ♂ MHND; PT ♀ MHND**	DOMINICAN REPUBLIC
Jaragua serranus Perez-Gelabert, Dominici & Hierro, 1995	HT ♂ ANSP; **PT unsexed MHND; PT immature MHND**	DOMINICAN REPUBLIC
Kapaoria flava Willemse, 1936	HT ♂ BMNH	INDONESIA
Kapaoria flavomaculata (Willemse, 1955)	**HT ♀ NBC**	INDONESIA
Kapaoria novaeguineae Bolívar, 1898	**HT ♂ MCSN**	INDONESIA
Katangacris enigmatica Kevan & Akbar, 1964	HT ♂ LEMQ	DEMOCRATIC REPUBLIC OF THE CONGO
Kuantania aptera Kevan, 1963	**HT ♀ NMW**	VIETNAM
Kuantania squamipennis Miller, 1935	**HT ♀ BMNH**	MALAYSIA
Laufferia chloronata (Bolívar, 1889)	**LT ♀ MNCN**	ANGOLA
Leptea albotaeniata (Werner, 1908)	**NT ♂ BMNH;**	LYBIA
Leptea debilis (Finot, 1894)	**LT ♂ MNHN**	ALGERIA
Loveridgacris impotens (Karsch, 1888)	**HT ♂ MfN**	TANZANIA
Macroleptea laevigata (Werner, 1914)	**PLT ♂ BMNH; PLT ♀ NHRS**	ALGERIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Malagasphena minor Kevan, Akbar & Singh, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MADAGASCAR
Marsabitacris citronota Kevan, 1957	**HT ♂ BMNH**	KENYA
Maura bolivari bolivari Kirby, 1902	**LT ♀ BMNH**	MALAWI
Maura bolivari fitzgeraldi Dirsh, 1954	**HT ♂ BMNH**	ZAMBIA
Maura bolivari modesta Bolívar, 1904	HT ♀ BMNH	TANZANIA
Maura lurida (Fabricius, 1781)	HT ♂ BMNH	Africa aequinoctialis
Maura marshalli Bolívar, 1904	LT ♂ UMO	ZIMBABWE
Maura rubroornata (Stål, 1855)	**T ♀ NHRS; T ♂ NHRS**	SOUTH AFRICA
Megalopyrga monochroma Baccetti, 1985	**HT ♀ Baccetti**	SOMALIA
Megra flava (Willemse, 1922)	**HT ♀ ZMAN**	INDONESIA
Megra trimaculata Willemse, 1955	**HT ♀ NBC**	INDONESIA
Megradina festiva Storozhenko, 2004	HT ♂ ZIN; **PT ♂ IBSS; PT ♀ IBSS**	VIETNAM
Mekongiana gregoryi (Uvarov, 1925)	**HT ♀ BMNH; PT ♂ BMNH**	CHINA
Mekongiana xiangchengensis Zheng, Huang & Zhou, 2008	HT ♂ Shaan♀i Normal	CHINA
Mekongiella kingdoni (Uvarov, 1937)	**HT ♀ BMNH; PT ♂ BMNH**	CHINA
Mekongiella pleurodilata Yin, 1984	T ♂ QIBX Xining	CHINA
Mekongiella rufitibia Yin, 1984	T ♂ QIBX Xining	CHINA
Mekongiella wardi (Uvarov, 1937)	**HT ♀ BMNH; PT ♂ BMNH**	CHINA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Mekongiella xizangensis Yin, 1984	T ♂ QIBX Xining	CHINA
Menesesia novaeguineae Willemse, 1922	**HT ♀ ZMAN**	PAPUA NEW GUINEA
Menesesiella occulta (Rehn, 1951)	**HT ♀ ANSP**	PAPUA NEW GUINEA
Menesesiella weylandi (Ramme, 1941)	**HT ♂ MfN; AT ♀ MfN**	INDONESIA
Meubelia atriantennis (Willemse, 1932)	**HT ♂ NHRS**	PHILIPPINES
Meubelia bakeri Kevan, 1967	HT ♂ USNM	PHILIPPINES
Meubelia bivittata Kevan, 1967	HT ♀ USNM	PHILIPPINES
Meubelia bruneri Kevan, 1967	HT ♂ USNM	PHILIPPINES
Meubelia gracilis Willemse, 1932	HT ♀ NHME; **2PT ♀ NHME; PT ♂ NHME**	PHILIPPINES
Meubelia leytensis Kevan, 1974	**HT ♂ ANSP; AT ♀ ANSP**	PHILIPPINES
Meubelia schistacra Kevan, 1967	HT ♂ BPBM	PHILIPPINES
Micropterus yongshengensis Dong & Wang, 2012	HT ? ISAS	CHINA
Minorissa pustulata Walker, 1870	**LT ♀ BMNH**	VENEZUELA
Minorissa volxemi (Bolívar, 1884)	**HT ♀ ISNB**	BRAZIL
Mitricephala dohrni (Bolívar, 1905)	**LT ♂ MNCN; PLT ♀ MNCN**	INDONESIA
Mitricephala javanica Kevan, 1963	**HT ♂ ANSP**	INDONESIA
Mitricephala milleri Ramme, 1941	HT ♂ BMNH	SINGAPORE
Mitricephala vittata Bolívar, 1898	**HT ♀ MCSN**	INDONESIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Mitricephaloides rhodopterus (Miller, 1934)	**HT ♀ BMNH**	MALAYSIA
Mitricephaloides rubrosignatus (Ramme, 1941)	**HT ♀ MfN**	BORNEO*
Modernacris callosa Uvarov, 1937	**HT ♀ BMNH**	SOLOMON ISLANDS
Modernacris carpentieri (Willemse, 1949)	**HT ♂ NHME**	SOLOMON ISLANDS
Modernacris controversa Willemse, 1931	HT ♀ NHMB	SOLOMON ISLANDS
Modernacris forcipata (Willemse, 1949)	**HT ♂ NHME**	SOLOMON ISLANDS
Modernacris guentheri (Ramme, 1941)	**HT ♀ MfN**	PAPUA NEW GUINEA
Modernacris simplex Willemse, 1935	**HT ♀ BMNH**	SOLOMON ISLANDS
Monistria cicatricosa Rehn, 1953	HT ♀ SAM	AUSTRALIA
Monistria concinna (Walker, 1871)	**HT ♀ BMNH**	AUSTRALIA
Monistria consobrina Key, 1985	**HT ♂ ANIC**	AUSTRALIA
Monistria discrepans (Walker, 1871)	**HT ♀ BMNH**	AUSTRALIA
Monistria latevittata Sjöstedt, 1921	HT ♀ ZMUH	AUSTRALIA
Monistria maculicornis Sjöstedt, 1921	**LT ♀ BMNH**	AUSTRALIA
Monistria pustulifera mallee Rehn, 1953	**HT ♂ ANIC**	AUSTRALIA
Monistria pustulifera pustulifera (Walker, 1871)	**HT ♀ BMNH**	AUSTRALIA
Monistria sulcata (Tepper, 1896)	**CT ♂ NHRS; CT ♀ NHRS**	AUSTRALIA
Neorthacris acuticeps acuticeps (Bolívar, 1902)	**LT ♂ MNHN; PLT ♂ MNCN; PLT ♀ MNCN**	INDIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Neorthacris acuticeps nilgirensis (Uvarov, 1929)	**HT ♂ MHNG**	INDIA
Neorthacris longicercata Singh & Kevan, 1965	**HT ♂ BMNH; AT ♀ BMNH**	INDIA
Neorthacris malabarensis Singh & Kevan, 1965	HT ♂ LEMQ	INDIA
Neorthacris palnensis (Uvarov, 1929)	**HT ♂ MHNG**	INDIA
Neorthacris simulans (Bolívar, 1902)	**LT ♂ MNHN; PLT ♂ MNCN; PLT ♀ MNCN**	INDIA
Nerenia francoisi Bolívar, 1905	**HT ♂ MNCN**	NEW CALEDONIA
Nilgiracris raoi (Kevan, 1953)	**HT ♂ BMNH; AT ♀ BMNH**	INDIA
Noonacris novahibernica Kevan, 1966	HT ♀ BPBM	PAPUA NEW GUINEA
Noonacris pusilla Kevan, 1966	**HT ♂ ZMUC**	PAPUA NEW GUINEA
Occidentosphena ruandensis (Rehn, 1914)	**HT ♀ MfN; AT ♂ MfN**	DEMOCRATIC REPUBLIC OF THE CONGO / RWANDA
Occidentosphena uvarovi (Rehn, 1942)	**HT ♂ ANSP; AT ♀ ANSP**	CAMEROON
Ochrophlebia cafra cafra (Linnaeus, 1764)	**NT ♂ UZIU**	SOUTH AFRICA
Ochrophlebia cafra ligneola (Serville, 1838)	**NT ♀ BMNH**	SOUTH AFRICA
Ochrophlegma pygmaea (Karsch, 1888)	**HT ♂ MfN**	MOZAMBIQUE
Ochrophlegma violacea (Stål, 1876)	**HT ♀ NHRS**	NAMIBIA
Ochrophlegma vittifera (Walker, 1871)	**HT ♀ BMNH**	SOUTH AFRICA
Omura congrua Walker, 1870	**LT ♀ BMNH**	BRAZIL

Table 2.4. Continued

Species or subspecies	Types	Type locality
Orthacris (*Orthacris*) *ceylonica* (Kirby, 1914)	**LT ♂ BMNH**	SRI LANKA
Orthacris (*Orthacris*) *comorensis* Singh & Kevan, 1965	**HT ♂ BMNH; AT ♀ BMNH**	INDIA
Orthacris (*Orthacris*) *curvicerca* Kevan, 1953	HT ♂ CNMS	SRI LANKA
Orthacris (*Orthacris*) *elongata* Kevan, 1953	HT ♂ CNMS	SRI LANKA
Orthacris (*Orthacris*) *filiformis* Bolívar, 1884	**LT ♂ NMW; PLT ♀ NMW**	SRI LANKA
Orthacris (*Orthacris*) *gracilis* Kevan, 1953	**HT ♂ BMNH; AT ♀ BMNH**	SRI LANKA
Orthacris (*Orthacris*) *maindroni* Bolívar, 1905	**LT ♀ MNHN; PLT ♀ MNCN**	INDIA
Orthacris (*Orthacris*) *major* Kevan, 1953	HT ♂ CNMS	SRI LANKA
Orthacris (*Pseudorthacris*) *elegans* Bolívar, 1902	**HT ♀ MNHN**	INDIA
Orthacris (*Pseudorthacris*) *incongruens* Carl, 1916	**HT ♂ MNHG**	INDIA
Orthacris (*Pseudorthacris*) *ramakrishnai* Bolívar, 1917	**HT ♀ MNCN**	INDIA
Orthacris (*Pseudorthacris*) *robusta* Kevan, 1953	**HT ♂ BMNH; AT ♀ BMNH**	INDIA
Orthacris (*Pseudorthacris*) *ruficornis* Bolívar, 1902	**LT ♂ MNHN; PLT ♀ MNHN; PLT ♂ MNCN; PLT ♀ MNCN**	INDIA
Paradoriaella tuberculata Willemse, 1961	**HT ♀ NBC**	INDONESIA
Paramekongiella zhongdianensis Huang, 1990	HT ♂ IZCAS	CHINA
Parapetasia femorata Bolívar, 1884	**HT ♀ NMW**	GABON
Paraphymateus roffeyi Dirsh, 1962	**HT ♀ BMNH**	SOMALIA
Parasphena campestris Rehn, 1942	**HT ♀ ANSP; AT ♂ ANSP**	KENYA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Parasphena cheranganica Uvarov, 1938	**HT ♂ MNHN**	KENYA
Parasphena chyuluensis Kevan, 1948	**HT ♀ BMNH; PT ♂ BMNH**	KENYA
Parasphena elgonensis Sjöstedt, 1933	**HT ♂ NHRS; AT ♀ NHRS**	KENYA
Parasphena hanangensis Hemp, 2009	HT ♂ MfN**; PT ♂ MfN; PT ♀ MfN**	TANZANIA
Parasphena imatongensis Rehn, 1942	**HT ♀ ANSP**	SUDAN
Parasphena kaburu Kevan, 1948	**HT ♀ BMNH**	KENYA
Parasphena keniensis keniensis Sjöstedt, 1912	**HT ♂ NHRS; PT ♀ NHRS**	KENYA
Parasphena keniensis rehni Kevan, 1956	**HT ♀ BMNH**	KENYA
Parasphena kinangopa Uvarov, 1938	**HT ♂ MNHN**	KENYA
Parasphena kulalensis Kevan, 1956	**HT ♂ BMNH**	KENYA
Parasphena mauensis kamasiensis Kevan, 1948	HT ♂ BMNH	KENYA
Parasphena mauensis mauensis Kevan, 1948	**HT ♀ BMNH**	KENYA
Parasphena meruensis meruensis Sjöstedt, 1910	**HT ♂ NHRS; PT ♀ NHRS; PT ♂ BMNH**	TANZANIA
Parasphena meruensis zeuneri Kevan, 1956	HT ♂ BMNH	TANZANIA
Parasphena nairobiensis Sjöstedt, 1933	**HT ♂ NHRS**	KENYA
Parasphena naivashensis Kevan, 1948	**HT ♀ BMNH; PT ♂ BMNH**	KENYA
Parasphena ngongensis Kevan, 1948	**HT ♀ BMNH; PT ♂ BMNH**	KENYA
Parasphena pulchripes (Gerstaecker, 1869)	**HT ♀ MfN**	TANZANIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Parasphena teitensis Kevan, 1948	**HT ♀ BMNH; PT ♂ BMNH**	KENYA
Parasphenella carinata (Bolívar, 1904)	**HT ♀ ETHZ**	SOUTH AFRICA
Parasphenella dubia (Bolívar, 1904)	**LT ♀ MNCN**	TANZANIA / KENYA
Parasphenella forchhammeri Johnsen & Kevan, 1984	HT ♂ LEMQ	TANZANIA
Parasphenella meridionalis (Kevan, 1956)	**HT ♀ BMNH**	LESOTHO
Parasphenula abyssinica (Uvarov, 1934)	**HT ♂ BMNH**	ETHIOPIA
Parasphenula boranensis (Salfi, 1939)	**NT ♀ MCSN**	ETHIOPIA
Parasphenula tewfiki (Uvarov, 1938)	HT ♂ BMNH	YEMEN
Parasphenula yemenita (Uvarov, 1936)	HT ♂ ZMUH; PT ♀ ZMUH	YEMEN
Parastria reticulata Key, 1985	**HT ♂ ANIC**	AUSTRALIA
Paratarbaleus novaeguineae (Ramme, 1930)	**HT ♂ MfN; PT ♀ MfN**	PAPUA NEW GUINEA
Paratarbaleus spinosus (Ramme, 1930)	**HT ♂ MfN**	PAPUA NEW GUINEA
Parorthacris somalica Dirsh, 1958	**HT ♂ BMNH**	SOMALIA
Petasida ephippigera White, 1845	**HT ♀ BMNH**	AUSTRALIA
Pezotagasta angolensis (Rehn, 1953)	**HT ♂ ANSP; AT ♀ ANSP**	ANGOLA
Pezotagasta bredoi Dirsh, 1961	**HT ♂ MRAC; 2 PT ♂ MRAC**	DEMOCRATIC REPUBLIC OF THE CONGO
Philippyrgus subapterus Kevan, 1974	**HT ♂ ANSP; AT ♀ ANSP**	PHILIPPINES
Phymateus (*Maphyteus*) *baccatus* Stål, 1876	**HT ♂ NHRS; AT ♀ NHRS**	NAMIBIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Phymateus (*Maphyteus*) *leprosus compressicollis* Bolívar, 1904	HT ♂ NHRS	
Phymateus (*Maphyteus*) *leprosus leprosus* (Fabricius, 1793)	NT ♂ BMNH	SOUTH AFRICA
Phymateus (*Phymateus*) *aegrotus* (Gerstaecker, 1869)	**HT ♀ MfN**	SOMALIA
Phymateus (*Phymateus*) *bolivari* Kirby, 1910	SOUTH AFRICA	
Phymateus (*Phymateus*) *cinctus* (Fabricius, 1793)	HT ♀ LSUK	SENEGAL
Phymateus (*Phymateus*) *iris* Bolívar, 1882	LT ♀ LZLP	ANGOLA
Phymateus (*Phymateus*) *karschi* Bolívar, 1904	**LT ♀ MfN, PLT ♂ MfN, PLT ♀ MfN**	MOZAMBIQUE
Phymateus (*Phymateus*) *madagassus* Karsch, 1888	**HT ♀ MfN**	MADAGASCAR
Phymateus (*Phymateus*) *morbillosus morbillosus* (Linnaeus, 1758)	**LT ♂ UZIU; 2 PLT ♂ UZIU**	Africa , Ïn Indis
Phymateus (*Phymateus*) *morbillosus sjostedti* Bolívar, 1904	**HT ♂ NHRS**	SOUTH AFRICA
Phymateus (*Phymateus*) *pulcherrimus* Bolívar, 1904	**LT ♂ MNCN; PLT ♂ MNCN**	ETHIOPIA
Phymateus (*Phymateus*) *saxosus* Coquerel, 1861	**HT ♀ MNHN; PT ♀ MNHN**	MADAGASCAR
Phymateus (*Phymateus*) *viridipes brunneri* Bolívar, 1884	**HT ♀ NMW**	ANGOLA
Phymateus (*Phymateus*) *viridipes viridipes* Stål, 1873	**ST ♀ NHRS; ST ♀ NHRS**	SOUTH AFRICA
Phymella capensis Uvarov, 1922	**HT ♂ BMNH; PT ♀ BMNH**	SOUTH AFRICA
Physemophorus sokotranus (Burr, 1898)	ST ♀ UMO; ST ♀ UMO	SOCOTRA
Phyteumas olivaceus (Karsch, 1896)	**HT ♀ MfN**	TANZANIA
Phyteumas purpurascens purpurascens (Karsch, 1896)	**LT ♀ MfN; PLT ♂ MfN**	TANZANIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Phyteumas purpurascens rufovenosis (Bolívar, 1922)	**HT ♂ MNHN**	KENYA
Phyteumas whellani Dirsh, 1953	HT ♂ BMNH	ZIMBABWE
Piscacris affinis Kevan, Singh & Akbar, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MEXICO
Piscacris robertsi Kevan, Singh & Akbar, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MEXICO
Plerisca peringueyi Bolívar, 1904	**HT ♀ MHNG**	SOUTH AFRICA
Plerisca rubripennulis (Key, 1937)	HT ♂ BMNH	SOUTH AFRICA
Plerisca sudindica Schmidt, 2004	HT ♀ Schmidt	INDIA
Poekilocerus arabicus Uvarov, 1922	**HT ♂ BMNH**	YEMEN
Poekilocerus bufonius bufonius (Klug, 1832)	**LT ♂ MfN; PLT ♀ MfN**	EGYPT
Poekilocerus bufonius hieroglyphicus (Klug, 1832)	**LT ♂ MfN; ALT ♀ MfN**	INDONESIA ??
Poekilocerus bufonius vittatus (Klug, 1832)	**LT ♂ MfN; PLT ♂ MfN**	INDONESIA
Poekilocerus calotropidis Karsch, 1888	**LT ♂ MfN; PLT ♀ MfN**	SUDAN
Poekilocerus geniplanus Gupta & Chandra, 2016	HT ♂ NZSI	INDIA
Poekilocerus pictus (Fabricius, 1775)	**HT ♀ ZMUC**	INDIA
Popovia salvadorae Uvarov, 1952	**HT ♂ BMNH; PT ♀ BMNH**	YEMEN
Propsednura eyrei Rehn, 1953	**HT ♂ ANIC**	AUSTRALIA
Propsednura peninsularis Key, 1972	**HT ♂ ANIC; PT ♂ BMNH**	AUSTRALIA
Prosphena scudderi Bolívar, 1884	**LT ♂ ANSP**	GUATEMALA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Protanita elongata (Bolívar, 1912)	**HT ♀ MRAC**	DEMOCRATIC REPUBLIC OF THE CONGO
Protanita fusiformis (Sjöstedt, 1929)	HT ♂ BMNH	TANZANIA
Protanita longiceps (Bolívar, 1904)	HT ♀ ZMUH	TANZANIA
Psedna nana (Rehn, 1953)	**HT ♀ ANIC**	AUSTRALIA
Psednura longicornis Sjöstedt, 1920	LT ♂NHRS	AUSTRALIA
Psednura musgravei Rehn, 1953	**HT ♂ ANIC; PT ♂ BMNH**	AUSTRALIA
Psednura pedestris (Erichson, 1842)	**LT ♂ MfN; ALT ♀ MfN**	AUSTRALIA
Pseudogeloius affinis Kevan, 1965	**HT ♂ MNCN; AT ♀ MNCN**	MADAGASCAR
Pseudogeloius decorsei (Bolívar, 1905)	**NT ♂ MNHN; NAT ♀ MNHN**	MADAGASCAR
Pseudogeloius fotadrevae Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Pseudogeloius marolintae Descamps & Wintrebert, 1966	**HT ♂ MNHN**	MADAGASCAR
Pseudogeloius relictus Dirsh, 1963	**HT ♂ MNHN; PT ♀ MNHN; PT ♂ BMNH; PT ♀ BMNH**	MADAGASCAR
Pseudomorphacris brachyptera Kevan, 1963	**HT ♂ ANSP; AT ♀ ANSP**	THAILAND
Pseudomorphacris hollisi Kevan, 1968	HT ♂ CAS	THAILAND
Pseudomorphacris notata (Brunner von Wattenwyl, 1893)	**LT ♂ MCSN**	MYANMAR
Pseudorubellia brancsiki (Bolívar, 1904)	**HT ♂ MNCN**	MADAGASCAR
Pseudorubellia thoracica geniculata Dirsh & Descamps, 1968	**HT ♂ MNCN; AT ♀ MNCN**	MADAGASCAR
Pseudorubellia thoracica thoracica Dirsh, 1963	**HT ♀ MNHN**	MADAGASCAR

Table 2.4. Continued

Species or subspecies	Types	Type locality
Pseudosphena dispar (Dirsh, 1963)	**HT ♂ MNHN; PT ♀ MNHN**	MADAGASCAR
Pterorthacris subcallosa Uvarov, 1921	**HT ♂ BMNH**	INDIA
Punctisphena pustulata Kevan, 1961	HT ♀ TMSA	ZIMBABWE
Pyrgohippus pallidus Dirsh, 1963	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Pyrgohippus productus (Descamps & Wintrebert, 1966)	**HT ♂ MNHN; AT ♀ MNHN; PT ♂ BMNH; PT♀ BMNH; PT ♀ MNCN**	MADAGASCAR
Pyrgomorpha (*Phymelloides*) *angolensis* Bolívar, 1889	**LT ♂ MNCN; PLT ♀ MNCN**	ANGOLA
Pyrgomorpha (*Phymelloides*) *granulata* Stål, 1875	**HT ♀ NHRS**	NAMIBIA
Pyrgomorpha (*Phymelloides*) *johnseni* Schmidt, 1999	HT ♀ Schmidt	ETHIOPIA
Pyrgomorpha (*Phymelloides*) *rugosa* (Key, 1937)	HT ♂ SAMC	SOUTH AFRICA
Pyrgomorpha (*Phymelloides*) *vignaudii semlikiana* (Rehn, 1914)	HT ♀ MfN	UGANDA / DEMOCRATIC REPUBLIC OF THE CONGO
Pyrgomorpha (*Phymelloides*) *vignaudii vignaudii* (Guérin-Méneville, 1847)	**NT ♀ MNHN**	ETHIOPIA
Pyrgomorpha (*Pyrgomorpha*) *agarena agarena* Bolívar, 1894	**LT ♂ MNCN; PLT ♀ MNCN**	MOROCCO
Pyrgomorpha (*Pyrgomorpha*) *agarena cyrenaicae* Kevan & Hsiung, 1988		LYBIA
Pyrgomorpha (*Pyrgomorpha*) *agarena zaeriana* Defaut, 1987	**HT ♂ MNHN; AT ♀ MNHN**	MOROCCO
Pyrgomorpha (*Pyrgomorpha*) *bispinosa bispinosa* Walker, 1870	**HT ♀ BMNH**	INDIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Pyrgomorpha (*Pyrgomorpha*) *bispinosa deserti* Bey-Bienko & Mistshenko, 1951	HT ♀ ZIN**; PT ♂ MNHN; PT ♀ MNHN**	UZBEKISTAN
Pyrgomorpha (*Pyrgomorpha*) *bispinosa incognita* Hsiung & Kevan, 1975	HT ♂ BMNH	MALI
Pyrgomorpha (*Pyrgomorpha*) *bispinosa mongolica* (Sjöstedt, 1933)	**HT ♀ NHRS**	MONGOLIA
Pyrgomorpha (*Pyrgomorpha*) *cognata captutorugosa* Hsiung, 1997	HT ♂ BMNH	SUDAN
Pyrgomorpha (*Pyrgomorpha*) *cognata caputagrava* Hsiung, 1997	HT ♂ BMNH	IRAN
Pyrgomorpha (*Pyrgomorpha*) *cognata cognata* Krauss, 1877	ST ♂ NMW	SENEGAL
Pyrgomorpha (*Pyrgomorpha*) *cognata kevani* Hsiung, 1997	HT ♂ BMNH	IRAN
Pyrgomorpha (*Pyrgomorpha*) *cognata maculifemur* Kevan, 1968	**HT ♂ MNHN; AT ♀ MNHN**	CHAD
Pyrgomorpha (*Pyrgomorpha*) *cognata minima* Uvarov, 1943	HT ♂ BMNH	EGYPT
Pyrgomorpha (*Pyrgomorpha*) *conica conica* (Olivier, 1791)	**NT ♀ MNHN**	FRANCE
Pyrgomorpha (*Pyrgomorpha*) *conica fusca* (Palisot de Beauvois, 1807)	NT ♀ LEMQ	GABON
Pyrgomorpha (*Pyrgomorpha*) *conica kurii* Hsiung & Kevan, 1975	HT ♂ BMNH	YEMEN
Pyrgomorpha (*Pyrgomorpha*) *conica pyrga* Steinmann, 1967	HT ♀ HNHM	CYPRUS
Pyrgomorpha (*Pyrgomorpha*) *conica tereticornis* (Brullé, 1840)	**HT ♀ MNHN**	CANARY ISLANDS
Pyrgomorpha (*Pyrgomorpha*) *cypria* Bolívar, 1901	**LT ♂ MNCN; PLT ♀ MNCN**	CYPRUS
Pyrgomorpha (*Pyrgomorpha*) *granosa* Stål, 1876	**HT ♀ NHRS; PT ♂ NHRS**	LEBANON
Pyrgomorpha (*Pyrgomorpha*) *guentheri* Burr, 1899	ST ♀ UMO	IRAN

Table 2.4. Continued

Species or subspecies	Types	Type locality
Pyrgomorpha (*Pyrgomorpha*) *hemiptera* Uvarov, 1938	HT ♂ BMNH	YEMEN
Pyrgomorpha (*Pyrgomorpha*) *inaequalipennis* Bolívar, 1904	**HT ♂ MHNG**	PAKISTAN ???
Pyrgomorpha (*Pyrgomorpha*) *lepineyi lepineyi* Chopard, 1943	**HT ♂ MNHN**	MOROCCO
Pyrgomorpha (*Pyrgomorpha*) *lepineyi montigena* Chopard, 1943	**ST ♂ MNHN; ST ♀ MNHN**	MOROCCO
Pyrgomorpha (*Pyrgomorpha*) *minuta* Kevan, 1963	**HT ♂ BMNH; PT ♀ BMNH**	SOUTH AFRICA
Pyrgomorpha (*Pyrgomorpha*) *tricarinata* Bolívar, 1884	**LT ♀ ISNB**	MOROCCO
Pyrgomorpha (*Pyrgomorpha*) *vosseleri* Uvarov, 1923	**HT ♀ BMNH**	ALGERIA
Pyrgomorphella albini (Chopard, 1921)	**HT ♀ MNHN**	KENYA
Pyrgomorphella arachidis Dirsh, 1951	**HT ♂ BMNH; PT ♀ BMNH; PT ♂ MNHN; PT ♀ MNHN**	TANZANIA
Pyrgomorphella carinulata Kevan, 1956	HT ♀ NMW	ERITREA
Pyrgomorphella dicrostachyae Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN; PT ♂ MNCN**	MADAGASCAR
Pyrgomorphella madecassa Bolívar, 1904	**LT ♀ MNHN**	MADAGASCAR
Pyrgomorphella minuta Dirsh, 1963	**HT ♂ MNHN; AT ♀ MNHN; PT ♂ MNCN**	MADAGASCAR
Pyrgomorphella rotundata Uvarov, 1936	**HT ♀ BMNH**	SAUDI ARABIA
Pyrgomorphella sphenarioides Bolívar, 1904	**LT ♀ MNHN**	ETHIOPIA
Pyrgomorphella tulearensis Descamps & Wintrebert, 1966	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Pyrgomorphellula curtula (Uvarov, 1952)	**HT ♂ BMNH; PT ♀ BMNH**	YEMEN

Table 2.4. Continued

Species or subspecies	Types	Type locality
Pyrgomorphula serbica (Pančić, 1882)	**ST ♂ MNCN; ST ♀ MNCN**	SERBIA
Pyrgotettix pueblensis Kevan, Singh & Akbar, 1964	**HT ♂ UMMZ; AT ♀ UMMZ**	MEXICO
Rakwana ornata Henry, 1933	**HT ♂ BMNH; PT ♀ BMNH**	SRI LANKA
Ramakrishnaia gracilis Kevan, 1964	**HT ♂ BMNH; AT ♀ BMNH**	INDIA
Ramakrishnaia notabilis Bolívar, 1917	**LT ♂ MNCN; PLT ♂ MNCN**	INDIA
Rubellia nigrosignata Stål, 1875	**HT ♀ NHRS; PT ♂ NHRS**	MADAGASCAR
Rutidoderes cinctus (Sjöstedt, 1929)	HT ♀ BMNH**; PT ♂ MfN; PT ♀ MfN**	DEMOCRATIC REPUBLIC OF THE CONGO
Rutidoderes concolor Kevan, 1962	HT ♂ CAS	CONGO
Rutidoderes squarrosus (Linnaeus, 1771)	**NT ♂ BMNH**	GHANA
Sagittacris malagassa Dirsh, 1963	**HT ♀ BMNH**	MADAGASCAR
Scabropyrgus scabrosus (Bolívar, 1889)	**LT ♀ MNCN; PLT ♀ MNCN**	ANGOLA
Schulthessia biplagiata Bolívar, 1905	**LT ♀ ETHZ**	MADAGASCAR
Scutillya verrucosa Sjöstedt, 1921	**LT ♂ BMNH; PLT ♀ BMNH**	AUSTRALIA
Shoacris bormansi (Bolívar, 1884)	**HT ♀ MNCN**	ETHIOPIA
Somalopyrgus messanai Baccetti, 1985	**HT ♂ Baccetti; AT ♀ Baccetti**	SOMALIA
Somalopyrgus rotundipennis Kevan & Akbar, 1964	**HT ♀ BMNH; AT ♂ BMNH**	SOMALIA
Sphenacris crassicornis Bolívar, 1884	**HT ♀ NMW**	MEXICO
Sphenarium adelinae Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO

Table 2.4. Continued

Species or subspecies	Types	Type locality
Sphenarium borrei Bolívar, 1884	**LT ♂ ISNB**	MEXICO
Sphenarium crypticum Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenarium histrio Gerstaecker, 1884	**HT ♂ MfN**	MEXICO
Sphenarium infernalis Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UMMZ	MEXICO
Sphenarium macrophallicum Kevan & Boyle, 1978	**HT ♂ UMMZ; AT ♀ UMMZ**	MEXICO
Sphenarium mexicanum Saussure, 1859	**LT ♀ MHNG; PLT ♂ MHNG**	MEXICO
Sphenarium minimum Bruner, 1906	**HT ♂ ANSP**	MEXICO
Sphenarium miztecum Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenarium occidentalis Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenarium planum Bruner, 1906	**LT ♂ ANSP**	MEXICO
Sphenarium purpurascens Charpentier, 1845	**LT ♂ MfN**	MEXICO
Sphenarium rugosum Bruner, 1906	**LT ♂ ANSP**	MEXICO
Sphenarium tarascum Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenarium totonacum Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenarium variabile Kevan & Boyle, 1978	**HT ♂ UMMZ; AT ♀ UMMZ**	MEXICO

Table 2.4. Continued

Species or subspecies	Types	Type locality
Sphenarium zapotecum Sanabria-Urbán, Song & Cueva del Castillo, 2017	HT ♂ UNAM	MEXICO
Sphenexia fusiformis Karsch, 1896	**HT ♂ MfN**	TANZANIA
Sphenotettix nobilis Kevan, Singh & Akbar, 1964	**HT ♂ ANSP; AT ♀ ANSP**	MEXICO
Spinacris elegans Kevan, 1966	HT ♀ BPBM	PHILIPPINES
Spinacris inermis Kevan, 1974	**HT ♀ ANSP**	PHILIPPINES
Spinacris viridis Willemse, 1933	**HT ♀ NHRS**	PHILIPPINES
Stenoscepa fusiformis (Kevan, 1956)	**HT ♂ BMNH**	TANZANIA
Stenoscepa gallae (Rehn, 1901)	**HT ♂ ANSP**	SOMALIA
Stenoscepa gracilis (Kevan, 1956)	**HT ♂ BMNH**	ZIMBABWE
Stenoscepa grandis (Kevan, 1956)	**HT ♀ BMNH**	KENYA
Stenoscepa granulata (Karsch, 1888)	**LT ♂ MfN; PLT ♀ MfN**	TANZANIA
Stenoscepa maxima (Kevan, 1948)	**HT ♀ BMNH; PT ♂ BMNH**	KENYA
Stenoscepa montana (Uvarov, 1934)	**HT ♂ BMNH**	ETHIOPIA
Stenoscepa obscura (Kevan, 1962)	**HT ♀ CAS**	ZIMBABWE
Stenoscepa picta (Bolívar, 1884)	**LT ♂ NMW; PLT ♀ NMW; PLT ♂ MNCN**	ETHIOPIA
Stenoscepa picticeps (Bolívar, 1904)	**HT ♂ MNCN**	SOUTH AFRICA
Stenoscepa rhodesiensis (Kevan, 1956)	**HT ♂ MRAC; AT ♀ MRAC; PT ♀ MRAC**	ZAMBIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Stenoxyphellus brachypterus Ramme, 1941	**HT ♀ MfN**	INDONESIA
Stenoxyphula excisa (Ramme, 1941)	**HT ♂ MfN; AT ♀ MfN**	INDONESIA
Stenoxyphula microphallica Kevan, 1966	HT ♂ BPBM	????
Stenoxyphus aurantiacus (Karsch, 1896)	**HT ♀ MfN**	INDONESIA
Stenoxyphus expansus Kevan, 1963	**HT ♂ BMNH; AT ♀ BMNH**	INDONESIA
Stenoxyphus variegatus (Blanchard, 1853)	**HT ♂ MfN**	INDONESIA
Stibarosterna serrata Uvarov, 1953	**HT ♀ BMNH; PT ♂ MNHN; PT ♀ MNHN**	ANGOLA
Tagasta anoplosterna (Stål, 1877)	**HT ♀ NHRS**	PHILIPPINES
Tagasta brachyptera Liang, 1988	T ♂ ICRI	CHINA
Tagasta celebesica (Karsch, 1888)	**HT ♂ MfN**	INDONESIA
Tagasta gui Yin, Ye & Yin, 2009	HT ♂ MHU	TAIWAN
Tagasta hoplosterna (Stål, 1877)	**HT ♀ NHRS; PT ♂ NHRS**	PHILIPPINES
Tagasta indica indica Bolívar, 1905	**LT ♂ MNCN; PLT ♀ MNCN**	BHUTAN
Tagasta indica mutata Rehn, 1953	**HT ♂ ANPS; AT ♀ ANSP**	THAILAND
Tagasta inornata (Walker, 1870)	**HT ♀ BMNH**	PHILIPPINES
Tagasta insularis Bolívar, 1905	**LT ♂ NMW**	INDONESIA
Tagasta longipenne Balderson & Yin, 1987		NEPAL
Tagasta marginella (Thunberg, 1815)	**HT ♂ UZIU**	INDONESIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Tagasta nigritibia Mao & Li, 2015	HT ♂ BMDU	CHINA
Tagasta rufomaculata Bi, 1983	HT ???	CHINA
Tagasta striatipennis Ramme, 1941	**HT ♀ MfN**	PHILIPPINES
Tagasta tonkinensis Bolívar, 1905	LT ♂ NMW	VIETNAM
Tagasta yunnana Bi, 1983	HT ???	CHINA
Tanita brachyptera Bolívar, 1912	**HT ♀ MRAC**	DEMOCRATIC REPUBLIC OF THE CONGO
Tanita breviceps (Bolívar, 1882)	**LT ♀ MNCN**	ANGOLA
Tanita lineaalba (Bolívar, 1889)	**LT ♂ MNCN; PLT ♀ MNCN**	ANGOLA
Tanita loosi loosi Bolívar, 1904	**LT ♀ ISNB**	DEMOCRATIC REPUBLIC OF THE CONGO
Tanita loosi pulchra Kevan, 1962	HT ♂ BMNH**; 2 PT ♂ ISNB; 3 PT ♀ ISNB**	DEMOCRATIC REPUBLIC OF THE CONGO
Tanita parva parva Kevan, 1962	**HT ♂ BMNH; AT ♀ BMNH**	TANZANIA
Tanita parva violacea Kevan, 1962	HT ♀ BMNH	SUDAN
Tanita purpurea Bolívar, 1904	HT ♀ BMNH	SOUTH AFRICA
Tanita rosea (Bolívar, 1908)	**HT ♀ ISNB**	DEMOCRATIC REPUBLIC OF THE CONGO
Tanita stulta Bolívar, 1912	**HT ♀ MRAC; PT ♂ MRAC**	DEMOCRATIC REPUBLIC OF THE CONGO
Tanita subcylindrica orientalis Kevan, 1962	**HT ♂ NMW; PT ♀ NMW**	TANZANIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Tanita subcylindrica subcylindrica (Bolívar, 1882)	**NT ♀ MNCN**	ANGOLA
Tanitella prasina (Karsch, 1888)	**HT ♀ MfN**	SOUTH AFRICA
Tanitella sanderi (Krauss, 1901)	HT ♀ SMNS	NAMIBIA
Taphronota (*Epamontor*) *cacuminata* Karsch, 1893	**HT ♀ MfN**	TOGO
Taphronota (*Epamontor*) *stali* Bolívar, 1884	**HT ♀ NHRS**	SOUTH AFRICA
Taphronota (*Taphronota*) *calliparea calliparea* (Schaum, 1853)	**ST ♂ MfN; ST ♀ MfN**	MOZAMBIQUE
Taphronota (*Taphronota*) *calliparea dimidiata* Bolívar, 1904	**LT ♀ MNHN; PLT unsexed MNHN**	ETHIOPIA
Taphronota (*Taphronota*) *ferruginea apicicornis* (Fairmaire, 1858)	**ST ♀ MNHN**	EQUATORIAL GUINEA
Taphronota (*Taphronota*) *ferruginea ferruginea* (Fabricius, 1781)	HT ♀ BMNH	"Africa aequinoctialis"
Taphronota (*Taphronota*) *grandis* Kevan, 1975	**HT ♀ BMNH**	TANZANIA
Taphronota (*Taphronota*) *merceti* Bolívar, 1904	**HT ♀ MNCN**	DEMOCRATIC REPUBLIC OF THE CONGO
Taphronota (*Taphronota*) *occidentalis* Karsch, 1892	**LT ♂ MfN; PLT ♀ MfN**	CAMEROON
Taphronota (*Taphronota*) *verrucosa* Kevan, 1975	HT ♀ CAS	DEMOCRATIC REPUBLIC OF THE CONGO
Tarbaleopsis brunnea (Willemse, 1955)	**HT ♂ NBC; AT ♀ NBC**	INDONESIA
Tarbaleopsis hystrix Kevan, 1966	HT ♂ BPBM	PAPUA NEW GUINEA
Tarbaleopsis minor Kevan, 1966	HT ♀ BPBM	INDONESIA
Tarbaleopsis proxima Kevan, 1968	HT ♀ BPBM	INDONESIA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Tarbaleopsis stellae Kevan, 1966	HT ♂ BPBM	INDONESIA
Tarbaleopsis tuberculata Ramme, 1930	**HT ♀ MfN**	INDONESIA
Tarbaleopsis willemsei Kevan, 1966	**HT ♂ NBC; AT ♀ NBC; PT ♂ NBC; 4 PT ♀ NBC**	INDONESIA
Tenuitarsus angustus (Blanchard, 1836)	HT ♀ UMO	EGYPT
Tenuitarsus orientalis Kevan, 1959	**HT ♀ BMNH; AT ♂ BMNH**	PAKISTAN
Tenuitarsus sudanicus Kevan, 1953	**HT ♂ BMNH; AT ♀ BMNH; PT ♂ MNHN**	SUDAN
Uhagonia depressa Dirsh, 1963	**HT ♀ MNHN**	MADAGASCAR
Uhagonia sphenarioides Bolívar, 1905	**HT ♀ NMW**	MADAGASCAR
Uhagonia wintreberti Kevan, 1968	**HT ♂ MNHN; AT ♀ MNHN**	MADAGASCAR
Verdulia cycloidea (Haan, 1842)	**ST ♀ NBC; ST ♀ NBC**	INDONESIA
Verdulia subcycloidea Willemse, 1932	**HT ♂ NBC; 2 PT ♀ NBC**	INDONESIA
Vittisphena somalica Kevan, 1956	**HT ♀ BMNH; AT ♂ BMNH**	SOMALIA
Xenephias socotranus Kevan, 1973	**HT ♂ BMNH; PT ♀ BMNH**	SOCOTRA
Xiphipyrgus tunstalli Kevan, 1982	**HT ♀ BMNH**	SOMALIA
Yeelanna argus (Rehn, 1953)	**HT ♀ ANIC**	AUSTRALIA
Yeelanna pavonina (Rehn, 1953)	**HT ♀ ANIC**	AUSTRALIA
Yunnanites albomargina Mao & Zheng, 1999	HT ♀ Shaanxi	CHINA
Yunnanites coriacea Uvarov, 1925	**HT ♂ BMNH**	CHINA

Table 2.4. Continued

Species or subspecies	Types	Type locality
Yunnanites zhengi Mao & Yang, 2003	T ?? CLDU	CHINA
Zarytes squalinus brachycerus (Kirby, 1914)	HT ♀ BMNH	INDIA
Zarytes squalinus squalinus (Saussure, 1884)	**HT ♀ NMW**	INDIA
Zonocerus elegans angolensis Kevan, 1972	**HT ♂ ANSP**	ANGOLA
Zonocerus elegans elegans (Thunberg, 1815)	**HT ♀ UZIU**	Africa
Zonocerus variegatus brachyptera Giglio-Tos, 1908	HT ♂ MIZT	
Zonocerus variegatus variegatus (Linnaeus, 1758)	**NT ♂ UZIU**	

Museum Codens (ordered by number of type material) following http://hbs.bishopmuseum.org/codens/

BMNH. The Natural History Museum, London, United Kingdom.

MNHN. Muséum National d'Histoire Naturelle, Paris, France.

MfN. Museum für Naturkunde, Berlin, Germany.

MNCN. Museo Nacional de Ciencias Naturales, Madrid, Spain.

ANSP. Academy of Natural Sciences of Drexel University, Philadelphia, USA.

NHRS. Naturhistoriska Riksmuseet, Stockholm, Sweden

NBC. Naturalis Biodiversity Center, Leiden, Netherlands.

NMW. Naturhistorisches Museum Wien, Austria.

BPBM. Bernice P. Bishop Museum, Honolulu, USA.

ANIC. Australian National Insect Collection, Canberra, Australia.

MHNG. Muséum d'Histoire Naturelle, Geneva, Switzerland.

CAS. California Academy of Sciences, San Francisco, USA.

ISNB. Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

MCSN. Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy.

UZIU. Uppsala University, Uppsala, Sweden.

LEMQ. Lyman Entomological Museum. Quebec, Canada.

USNM. National Museum of Natural History, Washington, USA.

MRAC. Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

NHME. Natuurhistorisch Museum, Maastricht, Netherlands.

UMO. University Museum, Hope Entomological Collections, Oxford, United Kingdom.

ZMUH. Zoologisches Institut und Zoologisches Museum, Hamburg, Germany.

CNMS. Colombo National Museum, Colombo, Sri Lanka.

ETHZ. Eidgenössische Technische Hochschule, Zürich, Switzerland.

IEAS. Institute of Entomology Academia Sinica, Shanghai, China.

QIBX. Qinghai Institute of Biology, Qinghai, China.

UMMZ. University of Michigan, Museum of Zoology, Ann Arbor, USA.

ZMUC. University of Copenhagen, Zoological Museum, Copenhagen, Denmark.

AMNH. American Museum of Natural History, New York, USA.

ICRI. Zhonghan University, Research Institute of Entomology, Guangdong, China.

MHU. Museum of Hebei University, China.

Schmidt. Schmidt Collection at Zoologische Staatssammlung München, Munich, Germany (ZSM).

Shaanxi. Institute of Zoology, Shaanxi Normal University, Shaanxi, China.

TMSA. Transvaal Museum, Pretoria, South Africa.

UNAM. Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Mexico City, Mexico.

ZMAN. Universiteit van Amsterdam, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam, Netherlands.

Baccetti. Baccetti Collection at Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (MCSN).

CLDU. Department of Life Sciences and Chemistry, Dali University, Dali, China.

HNHM. Hungarian Natural History Museum, Budapest, Hungary.

IZCAS. Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

MHND. Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic.

LSUK. Linnean Society, London, United Kingdom.

MSJC. St. Joseph's College, Natural History Museum, Tamil Nadu, India.

IBSS. Institute for Biology and Soil Science, Vladivostok, Russia.

NHMB. Naturhistorisches Museum, Basel, Switzerland.

SAM. South Australian Museum, Adelaide, Australia.

SAMC. South Africa Museum, Cape Town, South Africa.

Shandong. Department of Biology, Shandong University, Shandong, China.

SMNS. Staatliches Museum für Naturkunde, Stuttgart. Germany.

Stettin. Stettin Zoological Museum, Szczecin, Poland.

ZIN. Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia.

2.3.2 Museums visited

The vast majority of specimens are deposited in the insect collections of European and USA museums. Each museum has strengths in certain geographic areas and periods of time. This pattern was enhanced by orthopterologists working there or describing material from there. I briefly present some of these characteristics for the museums that I visited because this type of information is rarely reported in primary literature although it is immensely important for taxonomic research.

2.3.2.1 The Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, USA

Founded in 1812, ANSP contains more than 3.5 million specimens of insects of which more than 11,000 are primary types. Of those, 3,664 of them belong to the order Orthoptera. This high number is due to orthopterists such as Samuel H. Scudder (1837-1911), Lawrence Bruner (1856-1937), Joseph L. Hancock (1864-1922), James A.G. Rehn (1881-1965), Morgan Hebard (1887-1946), H. Radcliffe Roberts (??), and Daniel Otte (1939-present). Other orthopterists that have deposited type material are D. Rentz, D. Pérez-Gelabert, P. Naskrecki, M.M. Cigliano, K. McE. Kevan, and N.D. Jago among others.

Concerning Pyrgomorphidae, there are types of 26 valid species with K. McE. Kevan and his collaborators being the most prolific authors. The type collection is rich in material from Tropical Asia and especially from Mexico (fig. 2.6). In the last decades thanks to the effort of Daniel Otte, the collection of recent non-type material has positioned this collection as the most important both in coverage and the number of species for Pyrgomorphidae. A great majority of the pictures used in Chapter 3 were from the specimens housed in this museum.

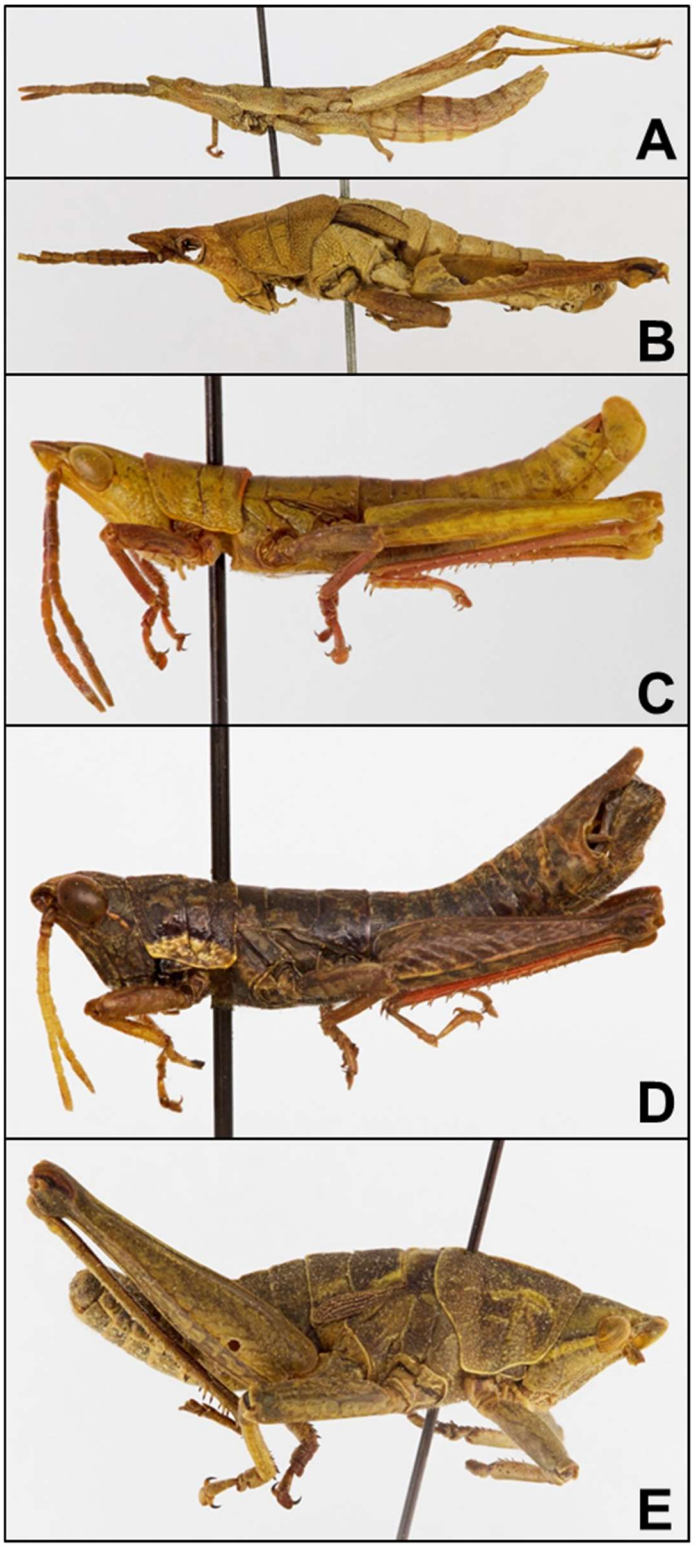

Figure 2.6. Pyrgomorphidae types from ANSP. **A.** *Calamacris clendoni* Rehn, 1904 (♂, LT); **B.** *Prosphena scudderi* Bolívar, 1884 (♂, LT); **C.** *Sphenotettix nobilis* Kevan, Singh & Akbar, 1964 (♂, HT); **D.** *Piscacris affinis* Kevan, Singh & Akbar, 1964 (♂, HT); **E.** *Sphenarium rugosum* Bruner, 1906 (♂, LT). All from Mexico except B (Guatemala).

2.3.2.2 Natural History Museum (BMNH), London, United Kingdom

Formerly known as the British Museum of Natural History, the Natural History Museum was founded in 1881. BMNH houses millions of insects for instance, 8 million specimens of Lepidoptera, 3 million specimens of Hymenoptera and 2.5 million specimens of Diptera. For Coleoptera it has type material of almost 100,000 species. Concerning Orthopteroids it houses 785,000 specimens in 4,639 drawers with 5,886 specimens as primary types. The Orthoptera collection comprises 378,000 specimens being 4,127 of those primary types. These numbers can be explained by Sir Boris P. Uvarov and Vitaly M. Dirsh who worked as the Orthoptera curators in the early 20th century, as well as the Anti-Locust Research Centre in London, which was the major center for grasshopper research, whose material was deposited at BMNH. There is also type material from J.C. Fabricius, F. Walker, C. Brunner von Wattenwyl, K. McE. Kevan, N.D. Jago, M. Descamps, A.V. Gorochov among others.

Concerning Pyrgomorphidae, there are types of 109 valid species. Walker, Uvarov, and Kevan were the most prolific authors. Although worldwide in scope, due to historical reasons associated with the colonical era of the British Empire, the great majority of the material came from countries such as Kenya and South Africa, Saudi Arabia, Yemen, India, Sri Lanka and Australia. Other countries of Africa, China and Papua Guinea are represented as well (Figs 2.7 and 2.8).

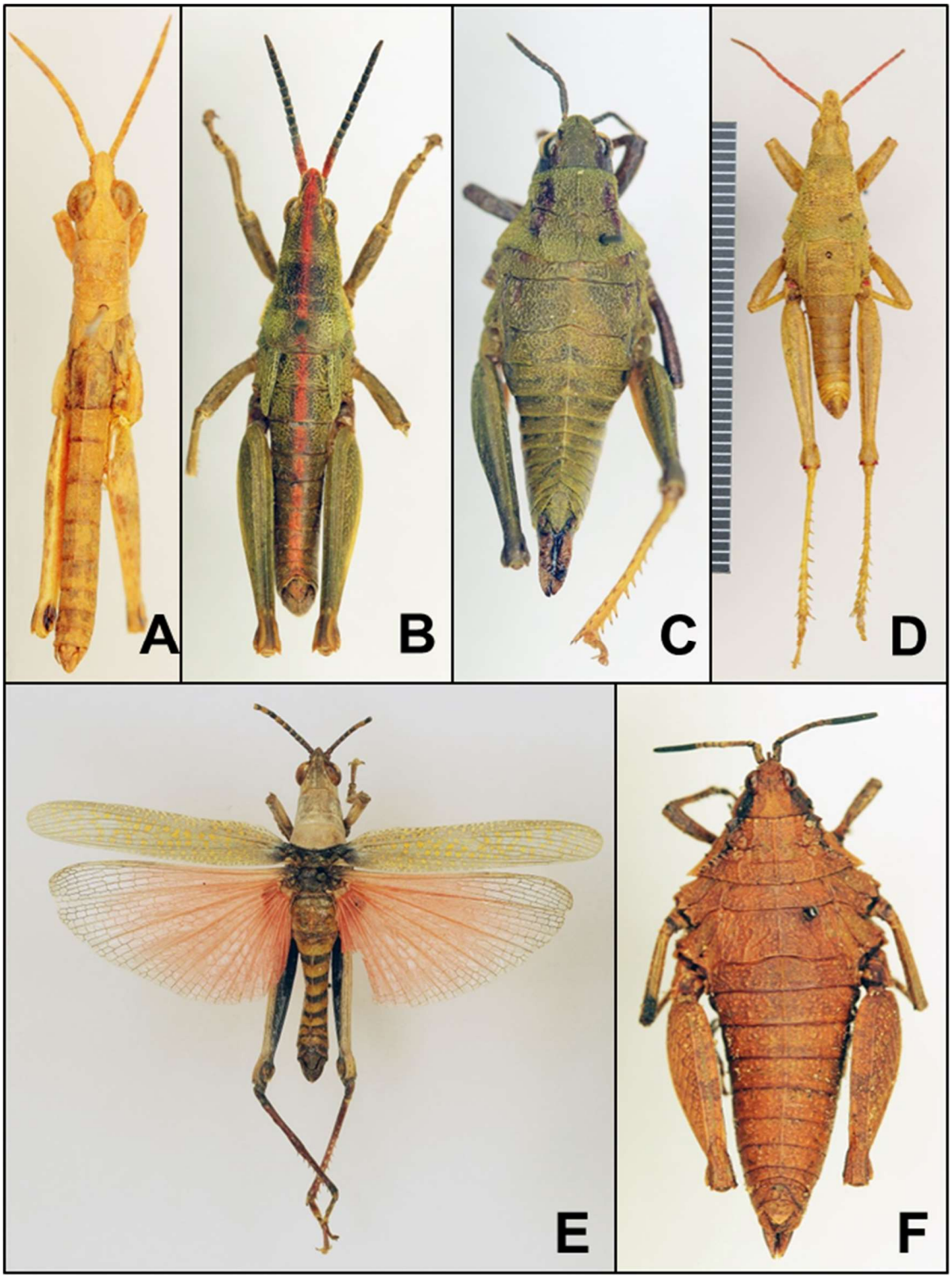

Figure 2.7. Pyrgomorphidae types from BMNH. **A.** *Popovia salvadorae* Uvarov, 1952 (♂, HT) Yemen; **B.** *Stenoscepa fusiformis* (Kevan, 1956) (♂, HT) Tanzania; **C.** *Mekongiella wardi* (Uvarov, 1937) (♀, HT) China; **D.** *Chirindites odendaali* Ramme, 1929 (♂, HT) Zimbabwe; **E.** *Poekilocerus arabicus* Uvarov, 1922 (♂, HT) Yemen; **F.** *Stibarosterna serrata* Uvarov, 1953 (♀, HT) Angola.

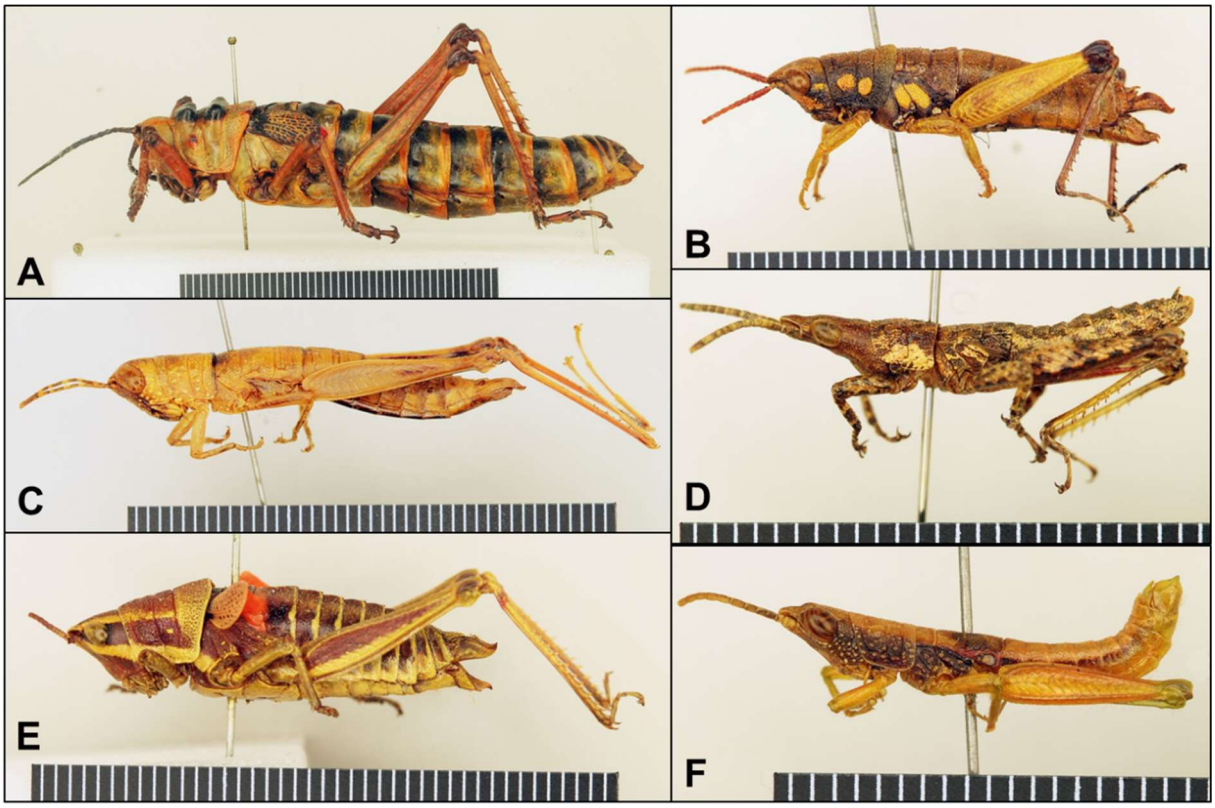

Figure 2.8. Pyrgomorphidae types from BMNH. **A.** *Paraphymateus roffeyi* Dirsh, 1962 (♀, HT) Somalia; **B.** *Kuantania squamipennis* Miller, 1935 (♀, HT) Malaysia; **C.** *Modernacris callosa* Uvarov, 1937 (♀, HT) Solomon Islands; **D.** *Xenephias socotranus* Kevan, 1973 (♂, HT) Yemen; **E.** *Monistria concinna* (Walker, 1871) (♀, HT) Australia; **F.** *Orthacris comorensis* Singh & Kevan, 1965 (♂, HT) India.

For each type specimen I took 3 photographs, dorsal and lateral views and labels (fig. 2.9), for the case of BMNH a number associated with the specimen was added to the labels pictures. Additionally, a scale was positioned next to the specimen in both lateral and dorsal pictures. The specimen in fig. 2.9 is the holotype of *Petasida ephippigera* and there is an interesting story behind this specimen. Key (1969) explained in detail why this specimen was the holotype and added the labels of holotype (red ringed) and the written explanation. In figure 2.10, three illustrations based on this specimen are provided. It is remarkable to be able to observe and photograph the holotype of such amazing grasshopper that has also been in this collection for 170 years and has been illustrated in different times.

Figure 2.9. *Petasida ephippigera* White, 1845 (♀, HT) Australia. **A.** Lateral view; **B.** Dorsal view; **C.** Labels.

The files were named following the protocols of BMNH. For instance in the case of the figure 2.9, the files were named:

Petasida_ephippigera_White_1845_holotype_female_lateral_BMNH_BMNH(E)#877228

Petasida_ephippigera_White_1845_holotype_female_dorsal_BMNH_BMNH(E)#877228

Petasida_ephippigera_White_1845_holotype_female_labels_BMNH_BMNH(E)#877228

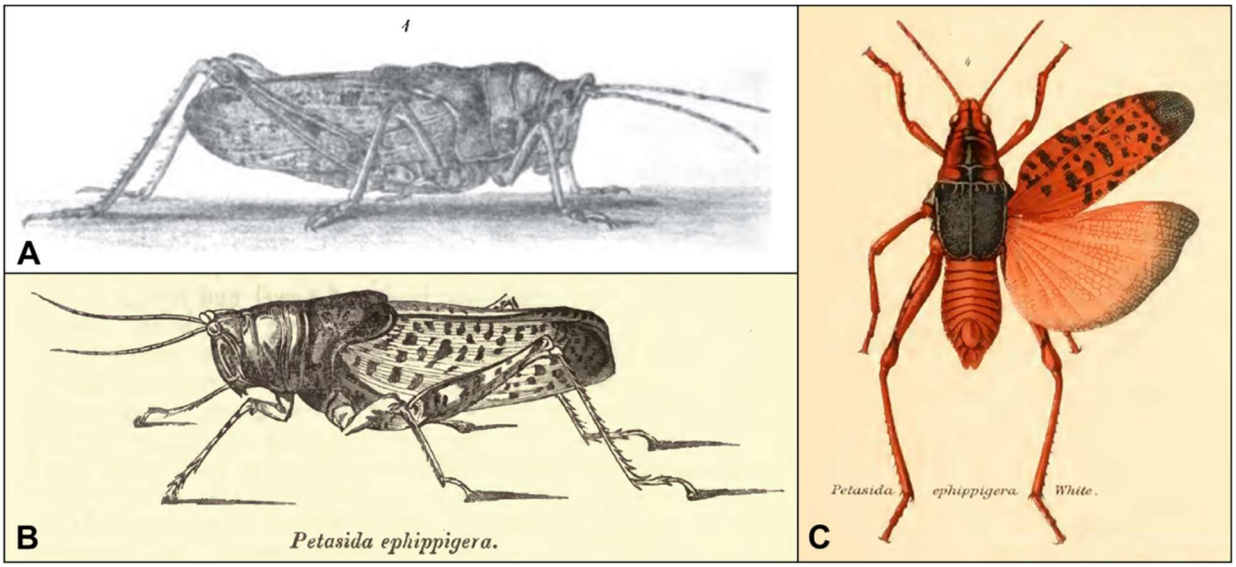

Figure 2.10. Illustrations of *Petasida ephippigera*. **A.** reprinted from White, 1845, page 432; **B.** reprinted from White, 1847, page 410; **C.** reprinted from Bolívar, 1909, fig 4, page 59.

This way of name files allows identifying them without seeing the images themselves. I realized the utility of this system, and since then I have used it to name my files. It also has the advantage when I am uploading all these pictures into Orthoptera Species File because it allows a faster uploading and an easy way to identify the files by me and other editors of OSF.

2.3.2.3 Muséum national d'historie naturelle (MNHN), Paris, France

Founded in 1793, MNHN houses 20 million specimens of Coleoptera, 7 million specimens of Hemiptera, 3 million specimens of Lepidoptera, 1 million specimens of Hymenoptera and 950,000 specimens of Orthopteroids orders with the great majority being Orthoptera and Blattodea. Concerning Orthoptera, 2,131 primary types are reported. The researchers associated with these numbers are E. Blanchard, L. Chopard, M. Descamps, C. Amédégnato, L. Desutter-Grandcolas, and T. Robillard. There is also type material of other authors such as J.G.A. Serville, I. Bolívar and A. Finot among others. Concerning Pyrgomorphidae, there are types of 72 valid species, most of which were described by Descamps and Wintrebert. Due to historical reasons the great majority of Pyrgomorphidae types are from Madagascar, although some from Mexico, India and continental Africa are present as well. In figure 2.11 a selection of Madagascar types is presented. It is remarkable that for the genus *Caprorhinus* from Madagascar, primary type material of 23 out of 28 species is deposited at MNHN, and for almost all of species the type series comprises dozens of paratypes of both sexes. As in BMNH, this museum provided an extra label with a number for each specimen in order to be included in the label photographs (figs. 2.11 and 2.12). This extra label will benefit the museum for database purposes and will save time for future references. Also as in BMNH, I present here two cases of very old specimens. The first case is the lectotype of *Dictyophorus griseus griseus* (fig. 2.12) and the illustration of the same specimen in the original work (Reiche & Fairmaire, 1849) (fig. 2.13). I was shocked with the similarities between the photograph (fig. 2.12C) and the drawing (fig. 2.13). The details in colors and patterns are extraordinary; the diminutive hind wings are exquisitely illustrated. It is hard to believe that these images are 165 years apart.

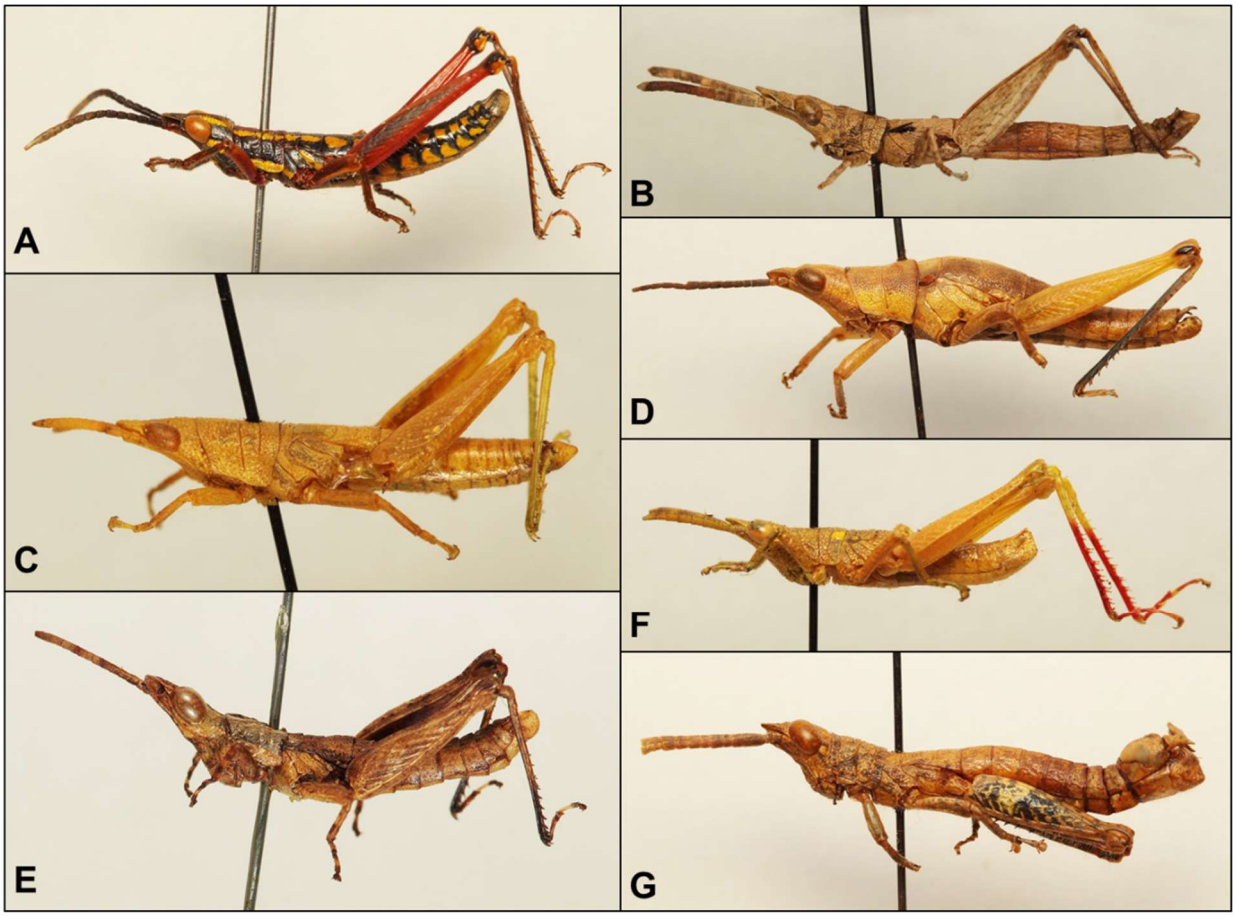

Figure 2.11. Madagascar type material from MNHN. **A.** *Pseudosphena dispar* (Dirsh, 1963) (♂, HT); **B.** *Geloius tanalanensis* Wintrebert, 1972 (♂, HT); **C.** *Pyrgohippus pallidus* Dirsh, 1963 (♂, HT); **D.** *Caprorhinus fotadrevensis* Kevan, Akbar & Chang, 1971 (♂, HT); **E.** *Pyrgomorphella minuta* Dirsh, 1963 (♂, HT); **F.** *Uhagonia wintreberti* Kevan, 1968 (♂, HT); **G.** *Pseudogeloius relictus* Dirsh, 1963 (♂, HT).

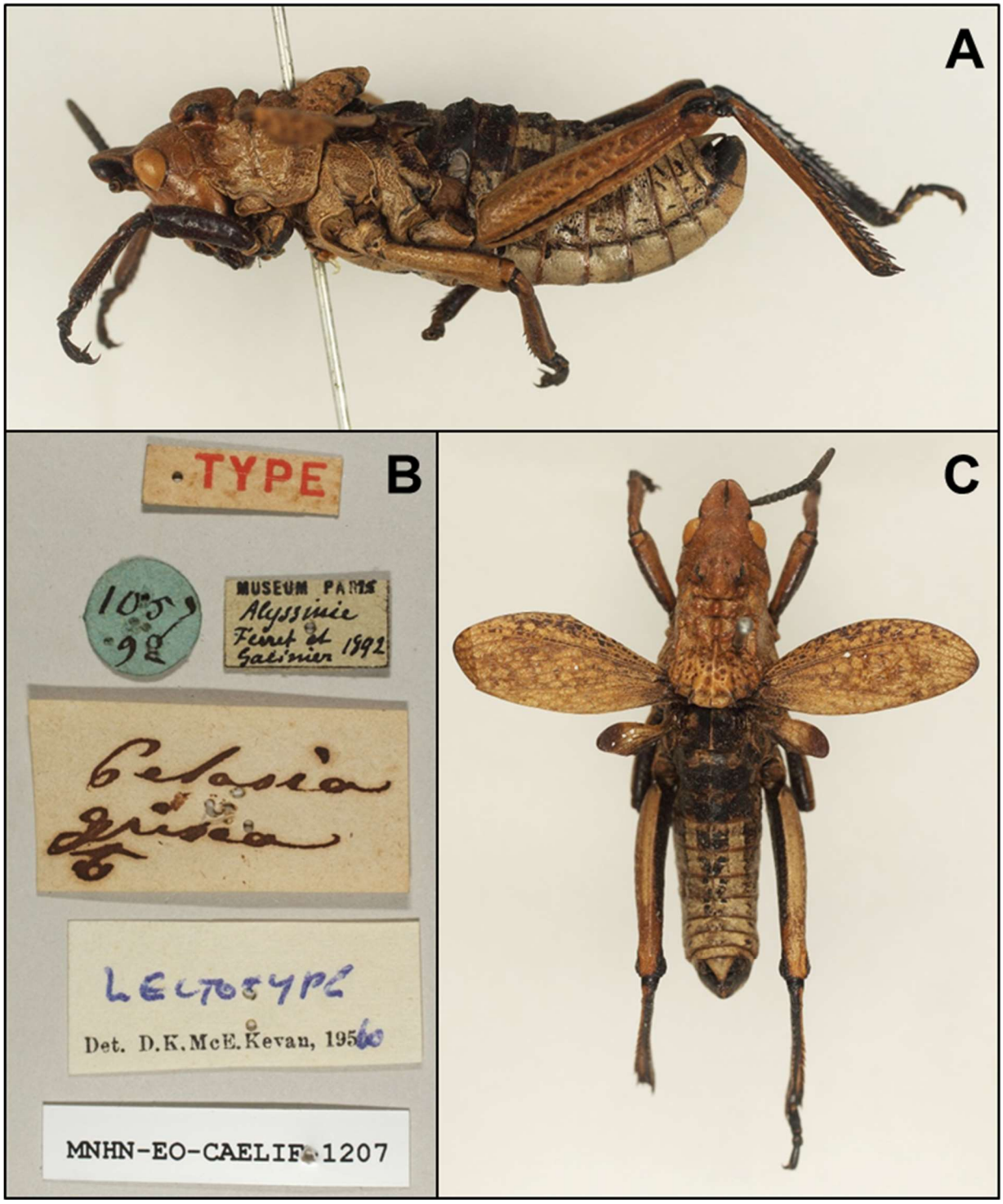

Figure 2.12. *Dictyophorus griseus griseus* (Reiche & Fairmaire, 1849) (♂, LT) Ethiopia. **A.** Lateral view; **B.** Labels; **C.** Dorsal view.

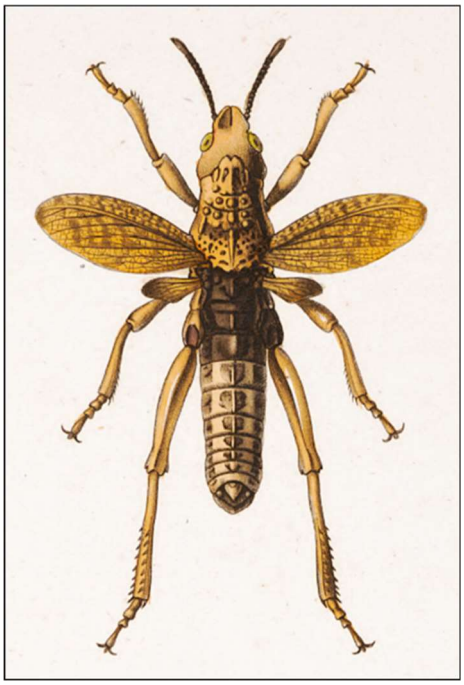

Figure 2.13. Illustration of *Dictyophorus griseus griseus* (as *Petasia grisea*) reprinted from Reiche & Fairmaire, 1849. Plate 28, fig. 2.

The second case is the holotype of *Chrotogonus homalodemus homalodemus* (fig. 2.14) and its illustration from the original work (Blanchard, 1836) (fig. 2.15). Although not in the same detail as the previous one, the illustration is remarkably accurate and based on the same specimen but made 178 years ago. For both species a lot of synonyms exist (13 for *D. g. griseus* and 7 for *C. h. homalodemus*) so it was imperative to have a photographic record for future revisions.

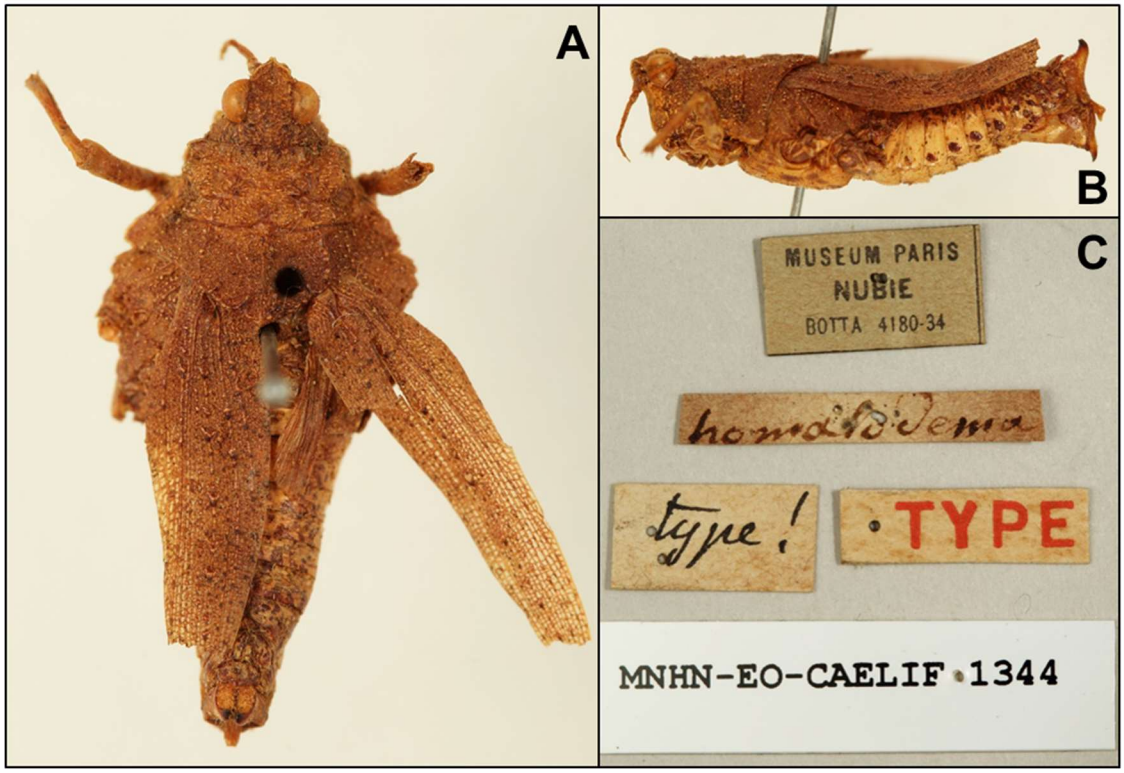

Figure 2.14. *Chrotogonus homalodemus homalodemus* (Blanchard, 1836) (♀, HT) Sudan. **A.** Dorsal view; **B.** Lateral view: **C.** Labels.

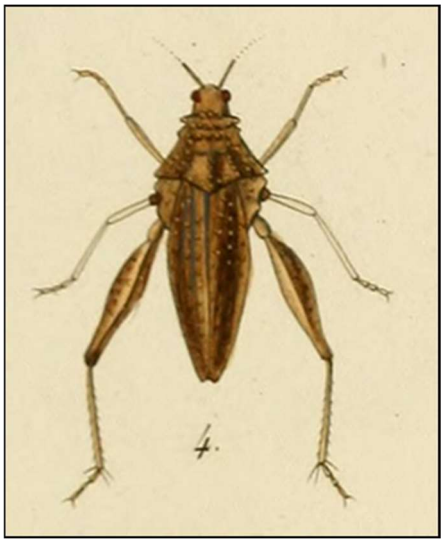

Figure 2.15. Illustration of *Chrotogonus homalodemus homalodemus* (as *Ommexecha homalodemum*) reprinted from Blanchard, 1836. Plate XXII, 4.

2.3.2.4 Museum für Naturkunde (MfN), Berlin, Germany

Established in 1810, MfN has more than 15 million specimens of insects. The orders Coleoptera (6 million), Lepidoptera (4 million), Hymenoptera (2.2 million), and Diptera (1.3 million) account for the 90% of the specimens. In the case of Orthoptera, there are 2,105 primary types. This number is due to descriptive works by C. Brunner von Wattenwyl, A. Gerstaecker, F.A.E. Karsch, K. Günther, W. Ramme, C. Bolívar, and more recently A.V. Gorochov, S. Ingrisch, and C. Hemp among others.

For Pyrgomorphidae, there is primary type material of 49 species. For historical reasons the great majority of the material is from Tanzania (part of Deutsch-Ostrafrika), Cameroon and Congo (part of Kamerun) and northern Papua New Guinea (Deutsch-Neuguinea). There are also material from other countries of Africa, Mexico and particularly other parts of Malesia (Philippines, Indonesia), many of which were described by Karsch and Ramme. In figures 2.16 and 2.17 some of the type diversity is presented.

As in the previous two museums, in figure 2.16, I present the three pictures taken per specimen. For the case of all the type material deposited at German Museums, an extra label from DORSA was added. DORSA stands for "**D**eutsche **Or**thopteren**sa**mmlungen" (German Orthoptera Collections in English). DORSA is a specimen-based database of Orthoptera collecions held in German Museums. One important characteristic of this database is that it is mutually linked with Orthoptera Species File so both are complementary. Before I started imaging the types, there were only 86 color images of Pyrgomorphidae types available that were made by Daniel Otte and DORSA.

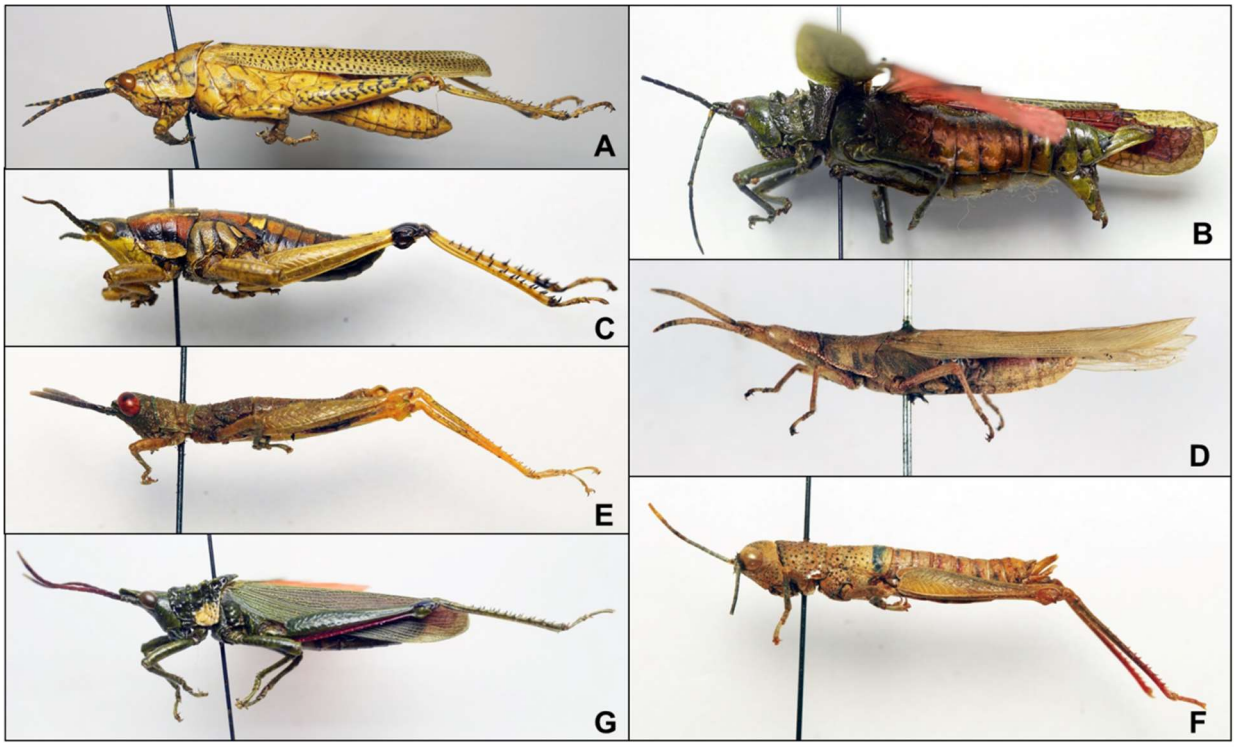

Figure 2.16. Pyrgomorphidae types from MfN. **A.** *Poekilocerus bufonius hieroglyphicus* (Klug, 1832) (♂, LT) Indonesia; **B.** *Taphronota cacuminata* Karsch, 1893 (♀, HT) Togo; **C.** *Sphenarium mexicanum histrio* Gerstaecker, 1884 (♂, ST) Mexico; **D.** *Atractomorpha angusta* Karsch, 1888 (♂, ST) Indonesia; **E.** *Buergersius olivaceus* Ramme, 1930 (♂, HT) Papua New Guinea; **F.** *Tarbaleopsis tuberculata* Ramme, 1930 (♀, HT) Papua New Guinea; **G.** *Taphronota occidentalis* Karsch, 1892 (♂, LT) Cameroon.

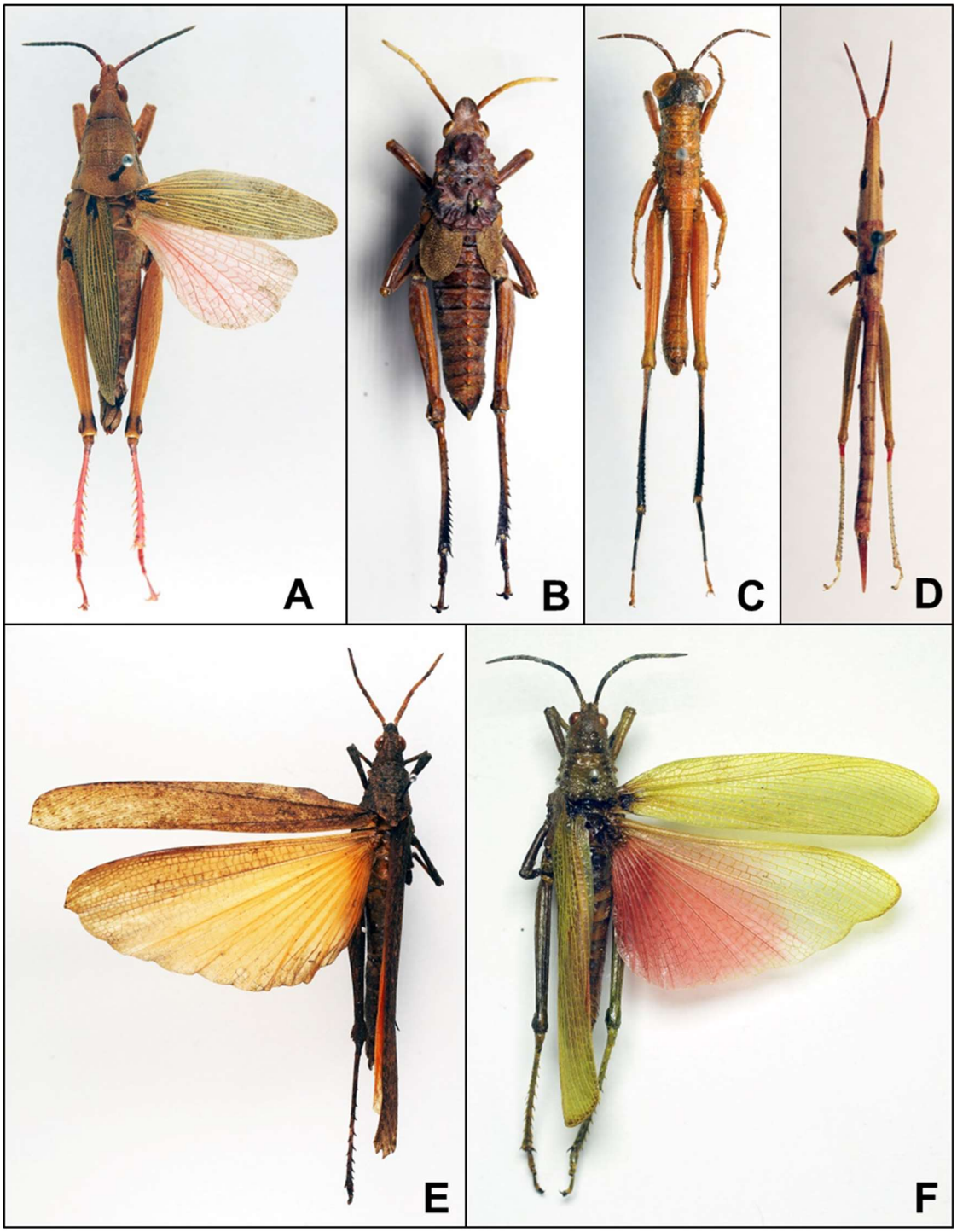

Figure 2.17. Pyrgomorphidae types from MfN. **A.** *Tagasta striatipennis* Ramme, 1941 (♀, HT) Philippines; **B.** *Loveridgacris impotens* (Karsch, 1888) (♂, HT) Tanzania; **C.** *Paratarbaleus novaeguinae* (Ramme, 1930) (♂, HT) Papua New Guinea; **D.** *Psednura pedestris* (Erichson, 1842) (♂, LT) Australia; **E.** *Stenoxyphus aurantiacus* (Karsch, 1896) (♀, HT) Papua New Guinea; **F.** *Phyteumas purpurascens purpurascens* (Karsch, 1896) (♂, LT) Tanzania.

In figure 2.18, two of the original illustrations of *Sphenarium purpurascens purpurascens* are shown. There is strong evidence that those drawings correspond to the lectotype (fig. 2.19). Kevan left a label indicating this relationship.

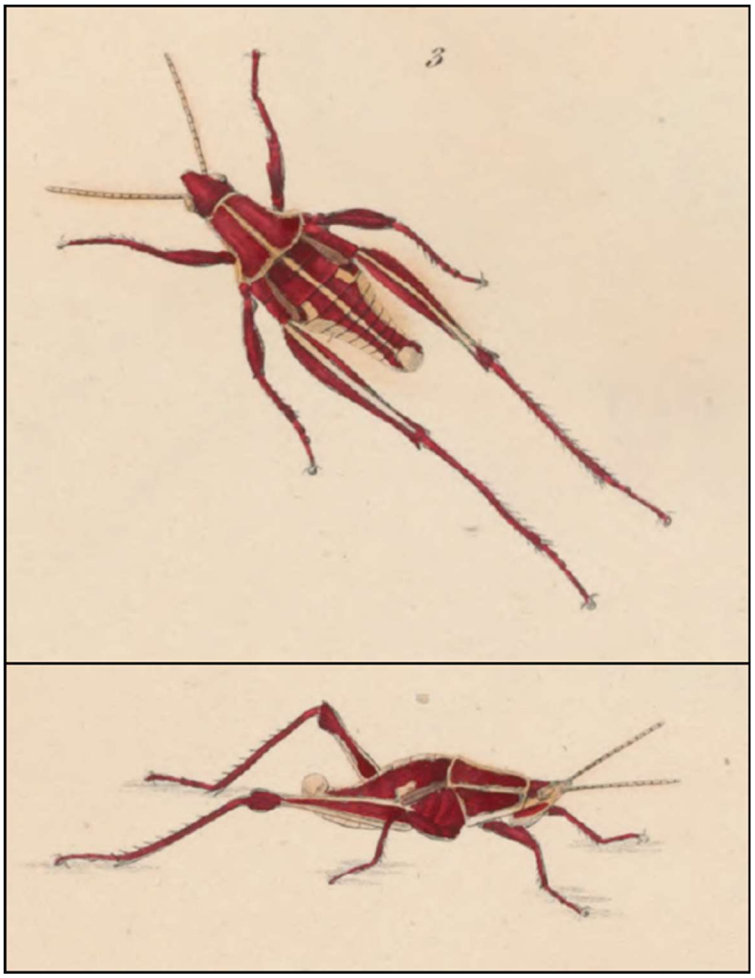

Figure 2.18. Illustrations of *Sphenarium purpurascens purpurascens* (as *Sphenarium purpurascens*) reprinted from Charpentier, 1845. Plate XXXI, 1,3.

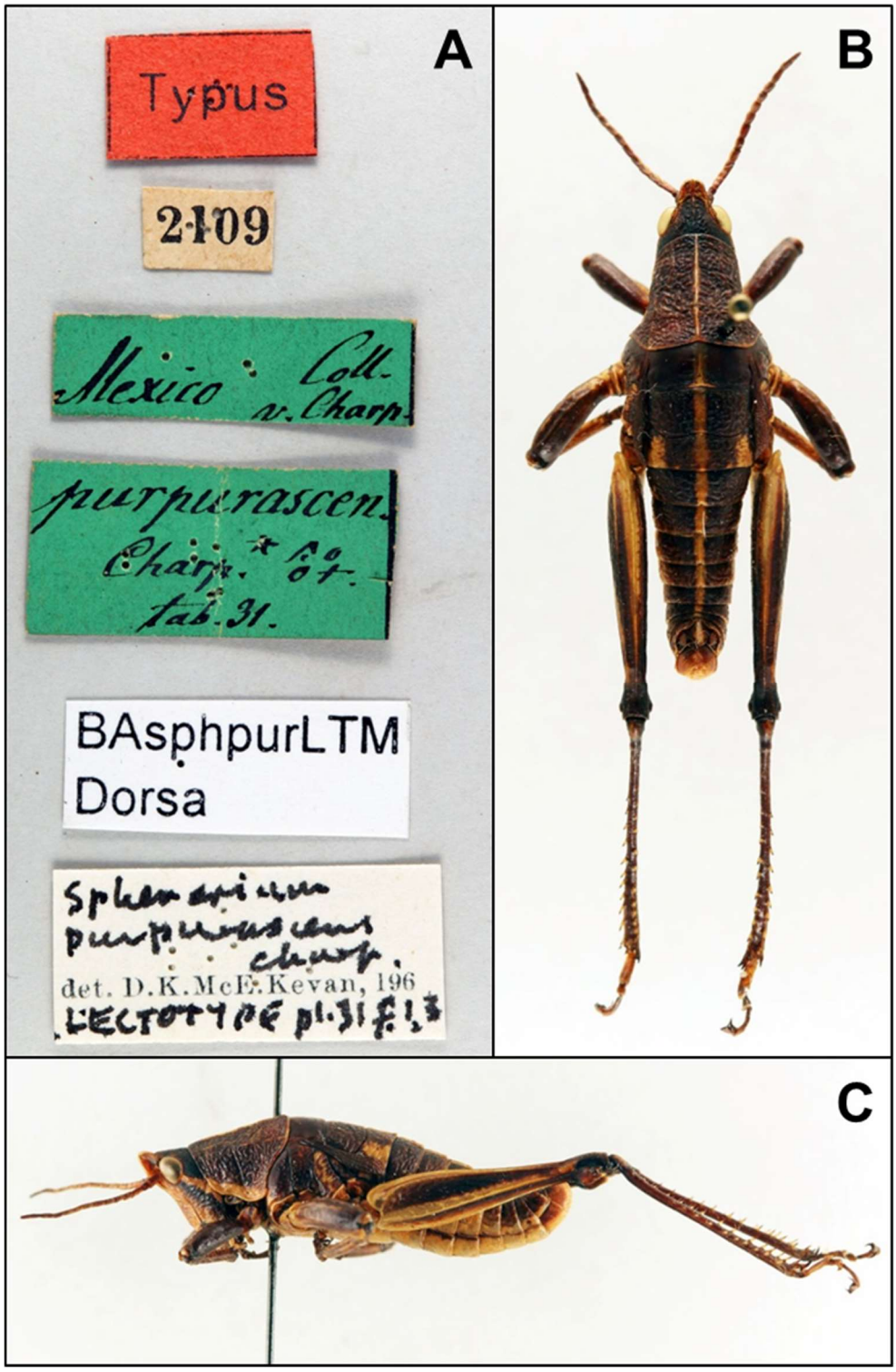

Figure 2.19. *Sphenarium purpurascens purpurascens* Charpentier, 1842 (♂, LT) Mexico. **A.** Labels; **B.** Dorsal view; **C.** Lateral view.

2.3.2.5 Museo Nacional de Ciencias Naturales, Madrid, Spain

Founded in 1771 by the King Carlos III, this museum houses more than 4 million specimens of insects. Concerning Orthoptera there are more than 100,000 pinned specimens with types of 1,005 taxa (including synonyms), 804 of them being currently valid taxa. This number is mainly due to the efforts of Ignacio Bolívar y Urrutia (1850-1944). Other Spanish orthopterologists also contributed, including Longinos Navás-Ferré (1858-1938), Manuel Cazurro Ruiz (1865-1935), Eugenio Morales-Agacino (1914-2002) and Vicenta Llorente del Moral (1930-). For historical reasons the areas covered in this collection are Spain and Canary Islands, Northern Africa, Equatorial Guinea, Philippines, South America, Madagascar, Minor Asia, and the Oriental Region.

In figure 2.20, lateral and dorsal views of some type material of Pyrgomorphidae described by Bolívar are shown. In figure 2.21 the three images obtained per specimen are shown. In several cases, Kevan designated lectotypes and paralectotypes because it was not usual during the 19th century to designate holotype and paratypes but only type or type series. However, in some cases Bolívar designated “the type” and then that specimen would become the holotype by original designation (article 73.1.1 ICZN). In other cases, Bolívar described the species based on a single specimen so in that case the holotype is fixed by monotypy (article 73.1.2 ICZN).

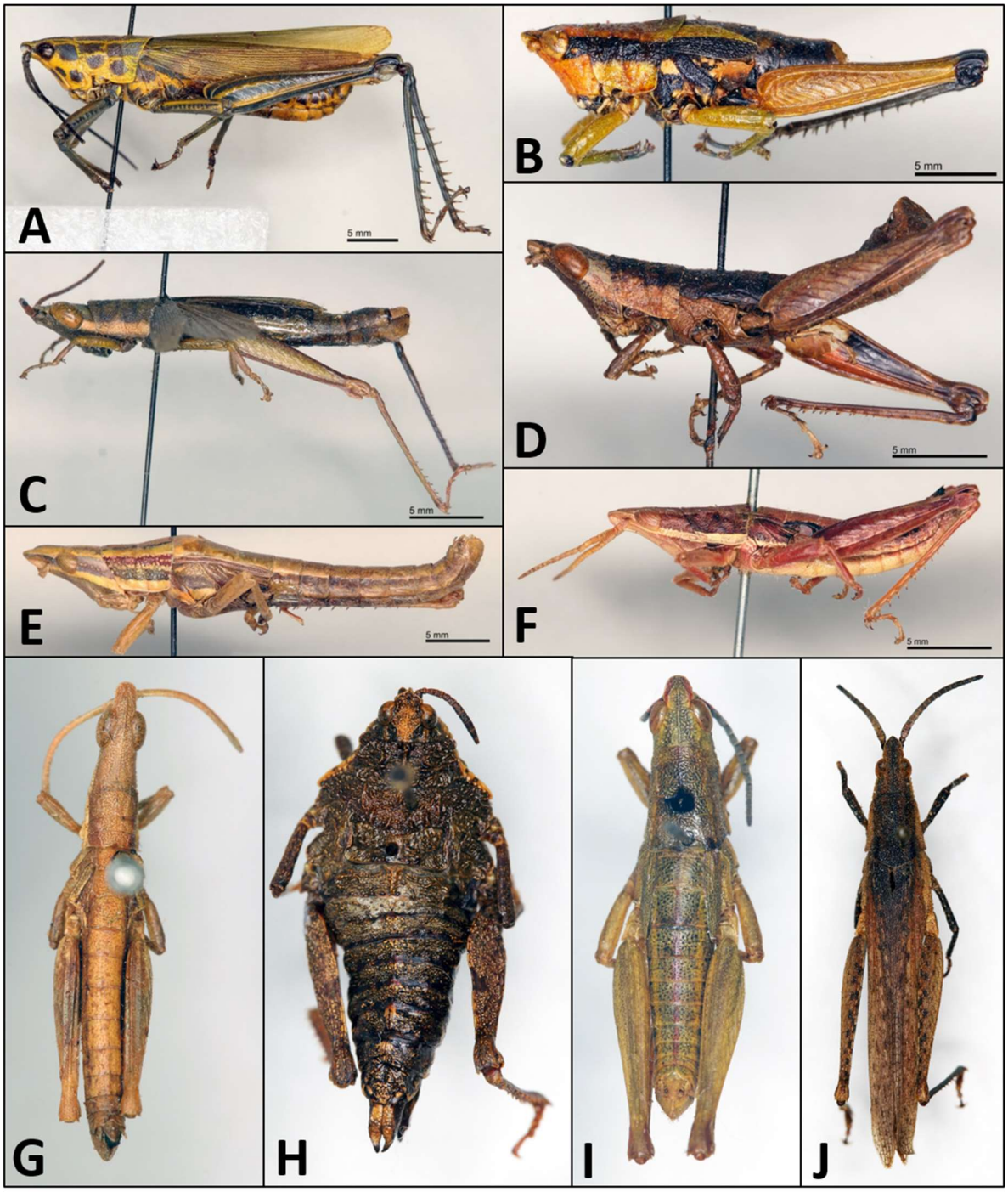

Figure 2.20. Pyrgomorphidae types from MNCN. **A.** *Annandalea robinsoni* Bolívar, 1905 (♂, HT) Malaysia; **B.** *Pseudorubellia brancsiki* (Bolívar, 1904) (♂, HT) Madagascar; **C.** *Mitricephala dohrni* (Bolívar, 1905) (♂, LT) Indonesia; **D.** *Nerenia francoisi* Bolívar, 1905 (♂, HT) New Caledonia; **E.** *Colemania sphenarioides* Bolívar, 1910 (♂, LT) India; **F.** *Ramakrishnaia notabilis* Bolívar, 1917 (♂, LT) India; **G.** *Anarchita aptera* (Bolívar, 1902) (♂, LT) India; **H.** *Shoacris bormansi* (Bolívar, 1884) (♀, HT) Ethiopia; **I.** *Stenoscepa picticeps* (Bolívar, 1904) (♂, HT) South Africa; **J.** *Tanita breviceps* (Bolívar, 1882) (♀, LT) Angola.

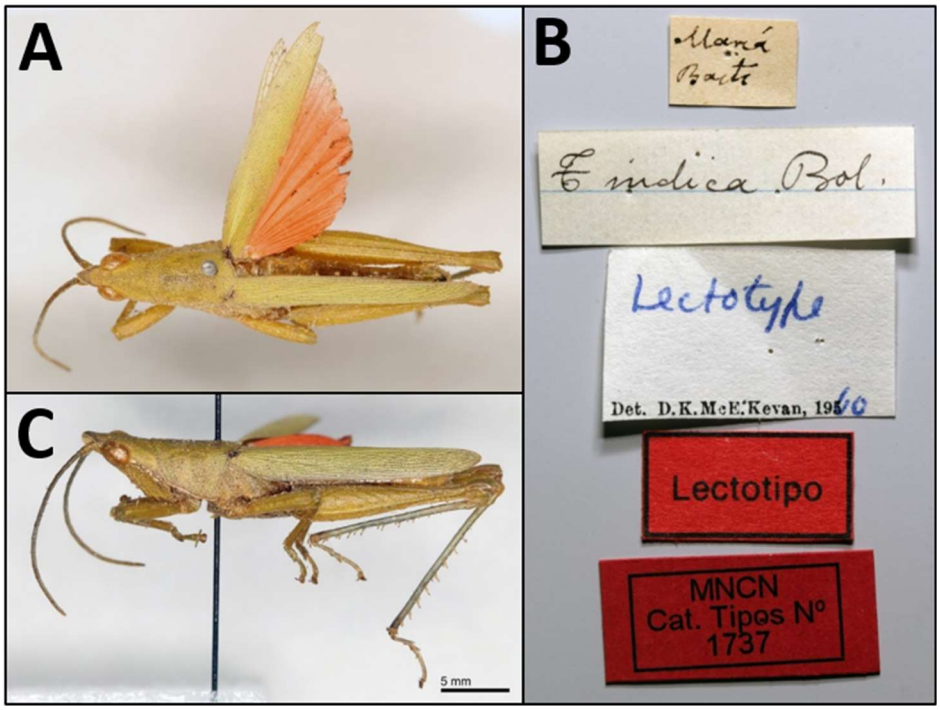

Figure 2.21. *Tagasta indica indica* Bolívar, 1905. (♂, LT) Bhutan. **A.** Dorsal view; **B.** Labels; **C.** Lateral view.

In figure 2.22, type material of two species are shown in dorsal view in order to show the wing coloration. This is very important because this part has information for phylogenetic analyses and it is not common to have type material like this (lectotype and holotype) with at least one tegmen and hindwing spread. Trying to spread tegmina and wings of type material is challenging and almost impossible.

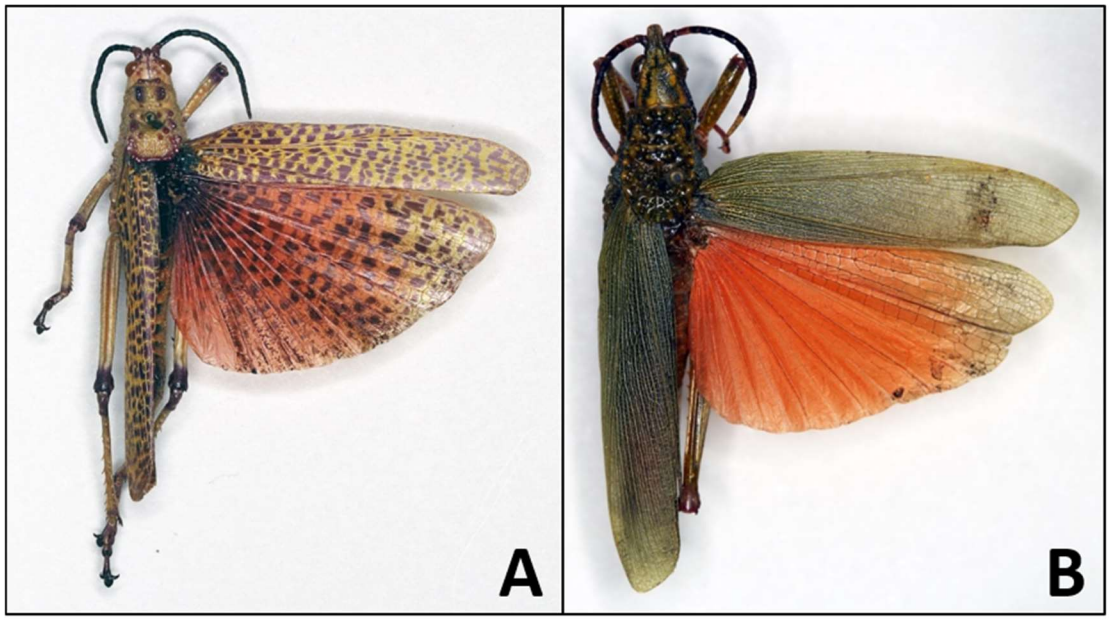

Figure 2.22. A. *Phymateus pulcherrimus* Bolívar, 1904 (♂, LT) Ethiopia; **B.** *Taphronota merceti* Bolívar, 1905 (♂, HT) Democratic Republic of the Congo.

In figure 2.23, some type material of species of Pyrgomorphidae not described by Bolívar are shown. It is of particular interest the second one (fig. 2.23B) because this species (*Pyrgomorphula serbica*) is critically endangered and its area of occupancy is estimated to be only 16 km^2 (Chobanov et al., 2016).

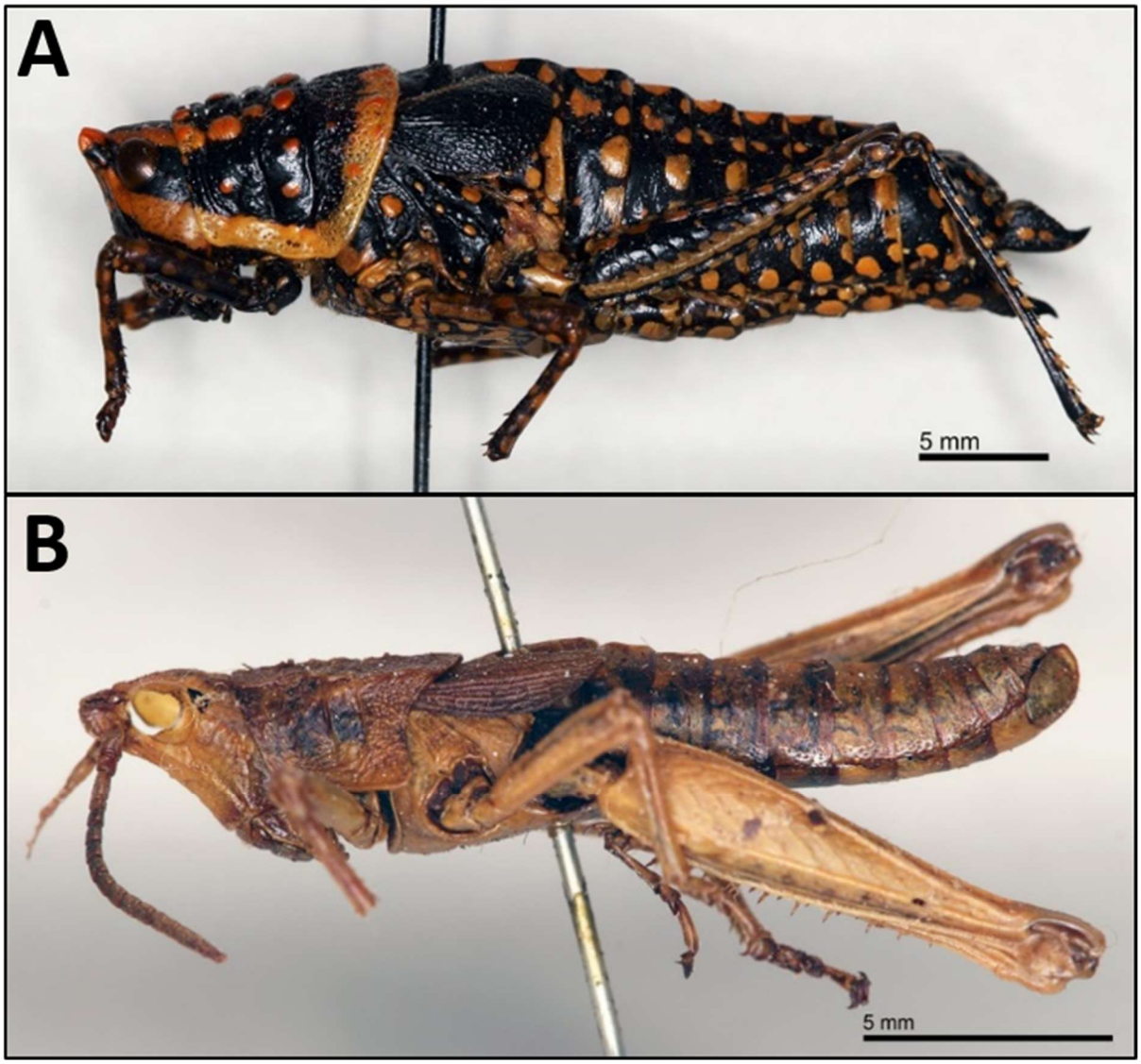

Figure 2.23. A. *Greyacris picta* (Sjöstedt, 1921) (♀, LT) Australia; **B.** *Pyrgomorphula serbica* (Pančić, 1882) (♂, ST) Serbia.

2.3.2.6 Muséum d'Histoire Naturelle (MHNG), Geneve, Switzerland

Founded in 1820 and with more than 15 million specimens, MHNG is the largest collection in Switzerland. The collections of Louis Jurine of Hymenoptera, Coleoptera, Lepidoptera and Hemiptera are held in the museum. Concerning Orthoptera, type material of 963 species (both valid and synonyms) are housed here mainly through the efforts of H. Saussure (1829-1905), C. Brunner von Wattenwyl (1823-1914), L. Redtenbacher (1814-1876), F.J. Pictet (1809-1872) among others. Although worldwide in scope, 346 out of 963 type species are from the Americas; this is mainly due to the expedition of Saussure to Mexico and the West Indies (1854-1856). However, Saussure's networking allowed him to describe species from other parts of the world as well, such as Madagascar, Asia, South America and Africa. Hollier & Hollier (2013) provided a very complete history of Saussure that helps to understand the collection of Geneve. For Pyrgomorphidae, there are type material from 24 species (both valid and synonyms) (figs. 2.24 & 2.25).

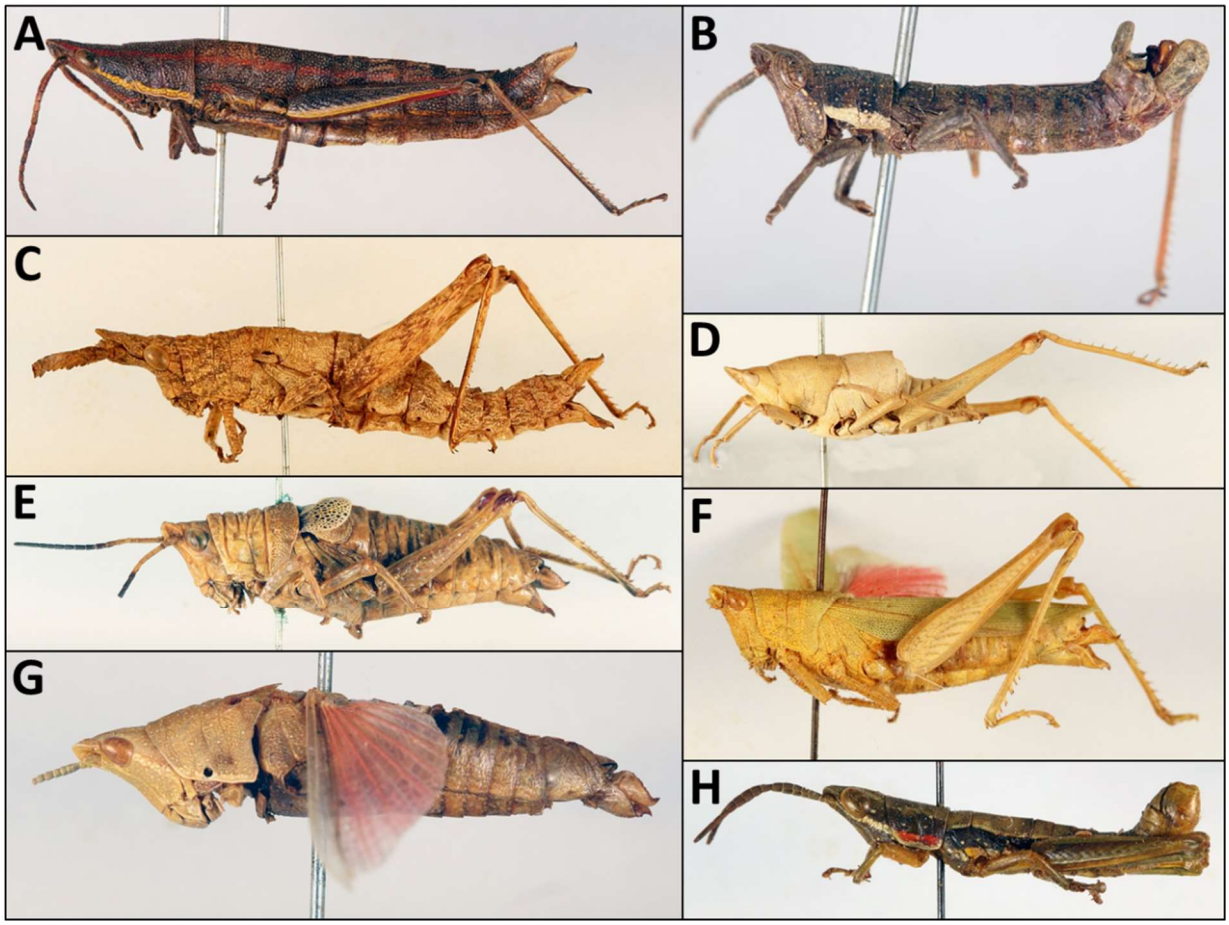

Figure 2.24. Pyrgomorphidae types from MHNG. **A.** *Dyscolorhinus squalinus* Saussure, 1899 (♀, LT) Madagascar; **B.** *Ichthyotettix mexicanus* (Saussure, 1859) (♂, LT) Mexico; **C.** *Geloius nasutus* Saussure, 1899 (♀, LT) Madagascar; **D.** *Sphenarium mexicanum* Saussure, 1859 (♀, LT) Mexico; **E.** *Greyacris profundesulcata* (Carl, 1916) (♀, HT) Australia; **F.** synonym *Pyrgomorpha capensis* Bolívar, 1904 (♀, HT) South Africa; **G.** *Pyrgomorpha inaequalipennis* Bolívar, 1904 (♀, PT); **H.** *Neorthacris acuticeps nilgirensis* (Uvarov, 1929) (♂, HT) India.

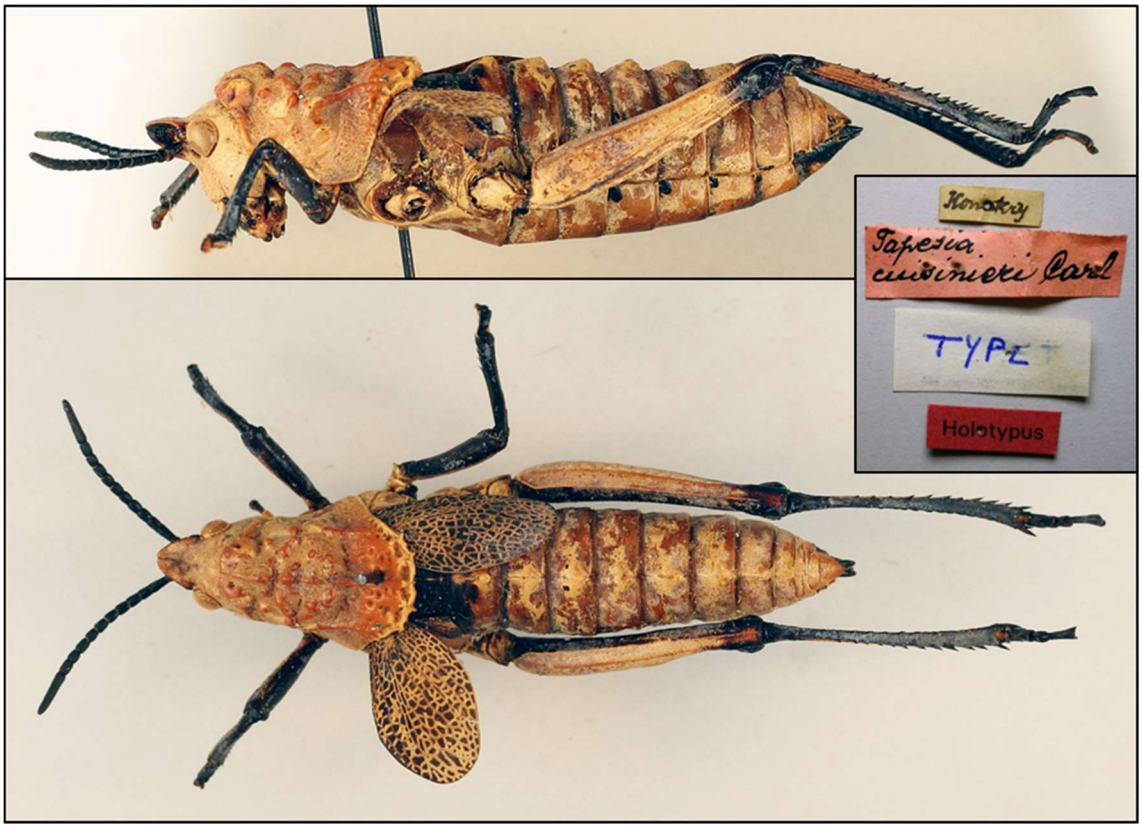

Figure 2.25. *Dictyophorus cuisinieri* (Carl, 1916) (♀, HT) Guinea (MHNG).

2.3.2.7 Eidgenössische Technische Hochschule (ETHZ), Zürich, Switzerland

The entomological collection of ETHZ holds more than 2 million specimens, including 5,200 primary types specimens. Concerning Orthoptera it holds type material of 21 species (both valid and synonyms). Regarding Pyrgomorphidae there are type material of six species (both valid and synonyms) (fig. 2.26). Among them, one of particular importance is the fossil *Myopyrgomorpha fischeri,* which is currently placed in Pyrgomorphidae but that was originally described as an acridid *Oedipoda fischeri*. The types are mainly from species described by A. V. Schulthess-Rechberg (end of 19th to beginning of 20th centuries) and I. Bolívar (1850-1949). It is precisely

Bolívar in 1905, who dedicated to Schulthess the Malagasy pyrgomorphid *Schulthessia biplagiata*.

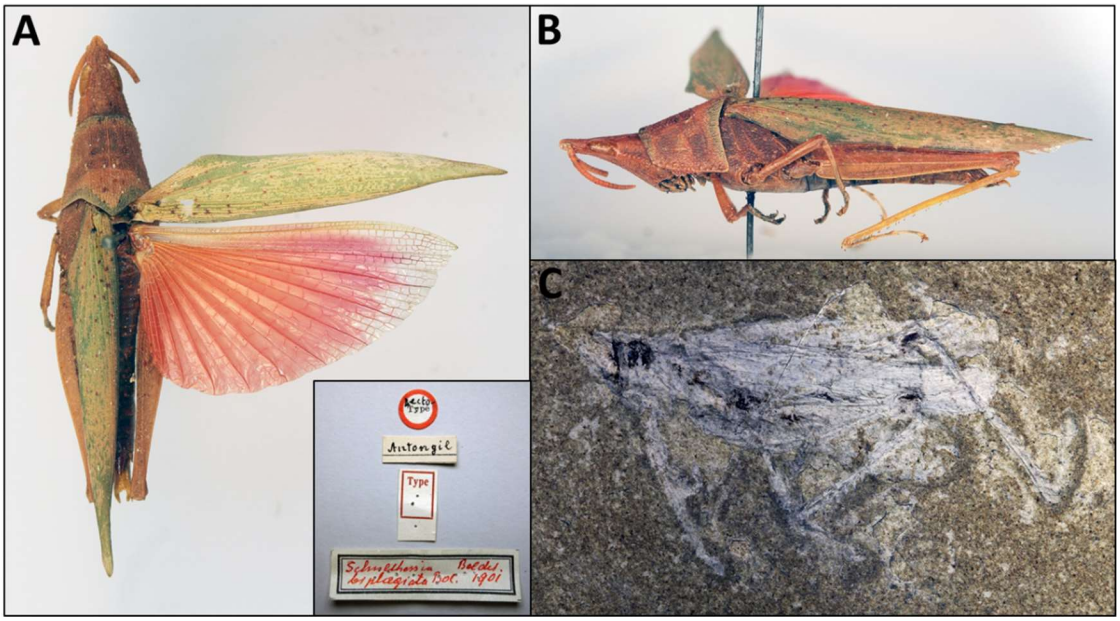

Figure 2.26. Pyrgomorphidae types from ETHZ. **A & B.** *Schulthessia biplagiata* Bolívar, 1905 (♀, LT) Madagascar; **C.** *Miopyrgomorpha fischeri* (Heer, 1865) (♂, HT) Germany (Miocene).

2.3.2.8 Naturhistorisches Museum (NMW), Wien, Austria

The insect collection of NMW holds more than 10 million specimens. Regarding Orthoptera, primary type material of 1,664 taxa (both valid and synonyms) are deposited here. This was primarily through the efforts of C. Brunner von Wattenwyl (1823-1914) (594 taxa) and L. Redtenbacher (1814-1876) (199 taxa). The collection is worldwide in scope (545 taxa are from Central and South America, 388 from Tropical Asia, 169 from Africa, 126 from Temperate Asia, 110 from Europe, 62 from Australasia, 52 from Pacific and, 39 from North America). Concerning Pyrgomorphidae there are type material of 32 species (both valid and synonyms) (figs. 2.27 & 2.28).

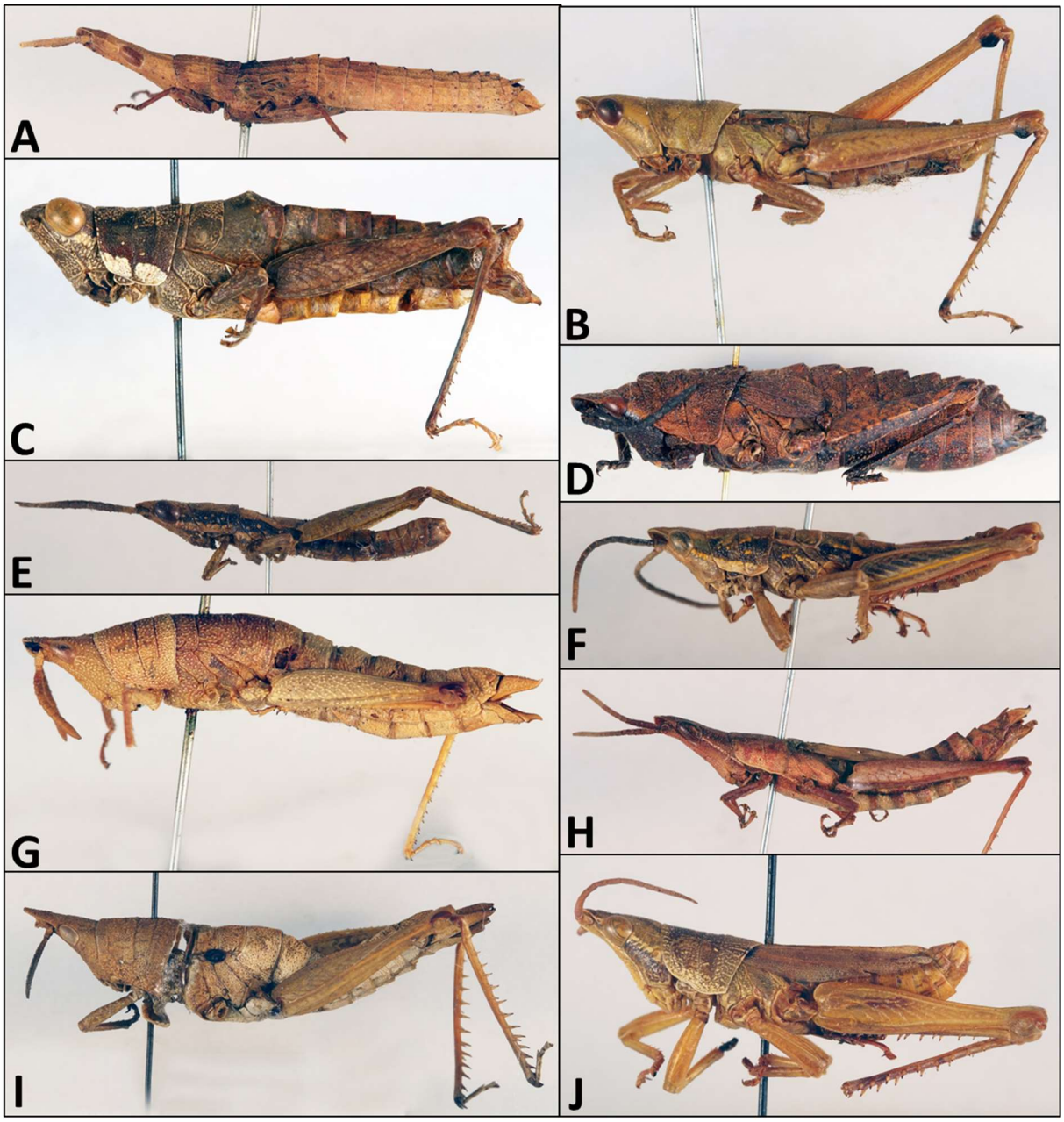

Figure 2.27. Pyrgomorphidae types from NMW. **A.** *Algete bunneri* Bolívar, 1905 (♀, HT) Brazil; **B.** *Chlorizeina unicolor unicolor* Brunner von Wattenwyl, 1893 (♂, ST) Myanmar; **C.** *Kuantania aptera* Kevan, 1963 (♀, HT) Vietnam; **D.** *Maura bolivari modesta* Bolívar, 1904 (♀, HT) Tanzania; **E.** *Orthacris filiformis* Bolívar, 1884 (♂, LT) Sri Lanka; **F.** *Stenoscepa picta* (Bolívar, 1884) (♂, LT) Ethiopia; **G.** *Sphenacris crassicornis* Bolívar, 1884 (♀, HT) Mexico; **H.** *Zarytes squalinus squalinus* (Saussure, 1884) (♀, HT) India. **I.** *Uhagonia sphenarioides* Bolívar, 1905 (♀, HT) Madagascar; **J.** *Tagasta insularis* Bolívar, 1905 (♂, LT) Indonesia.

Figure 2.28. *Parapetasia femorata* Bolívar, 1884 (♀, HT) Gabon (NMW).

2.3.2.9 Naturhistoriska Riksmuseet (NHRS), Stockholm, Sweden

The entomological collection of NHRS holds more than 3 million of specimens. Regarding Orthoptera, 1,062 taxa (both valid and synonyms) are deposited here. This collection is very historical and worldwide in scope thanks to the efforts of C. De Geer (1720-1778) (42 taxa), C. Stål (1833-1878) (407 taxa), B.Y. Sjöstedt (1866-1948) (412 taxa) and L. Chopard (1885-1971) (55 taxa) among others. Concerning Pyrgomorphidae, there are type material of 64 species (both valid and synonyms) (figs. 2.29 & 2.30).

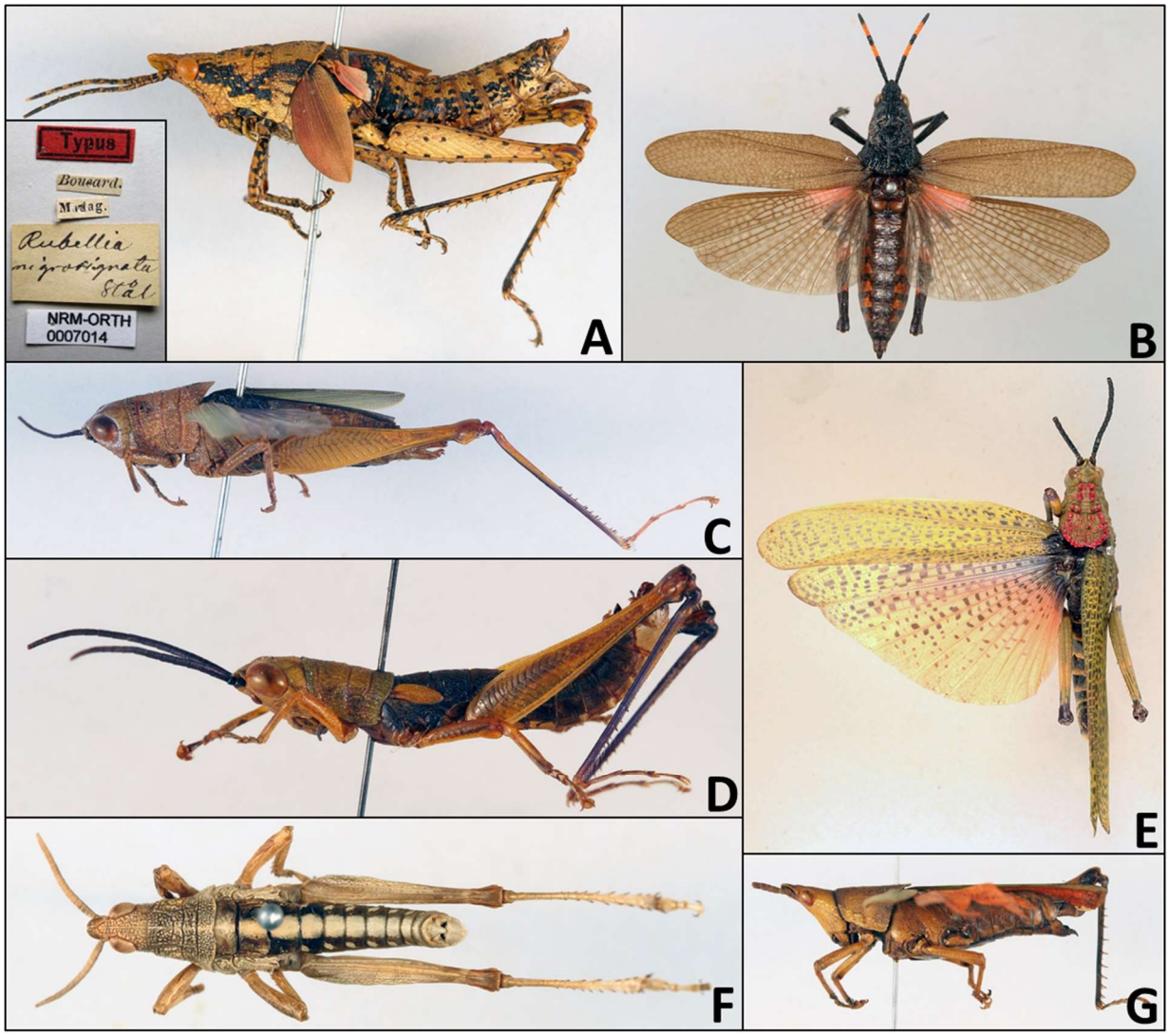

Figure 2.29. Pyrgomorphidae types from NHRS. **A.** *Rubellia nigrosignata* Stål, 1875 (♀, HT) Madagascar; **B.** *Maura rubroornata* (Stål, 1855) (♂, ST) South Africa; **C.** *Spinacris viridis* Willemse, 1933 (♀, HT) Philippines; **D.** *Meubelia atriantennis* (Willemse, 1932) (♂, HT) Philippines; **E.** *Phymateus morbillosus sjostedti* Bolívar, 1904 (♂, HT) South Africa; **F.** *Parasphena nairobiensis* Sjöstedt, 1933 (♂, HT) Kenya; **G.** *Tagasta hoplosterna* (Stål, 1877) (♀, HT) Philippines.

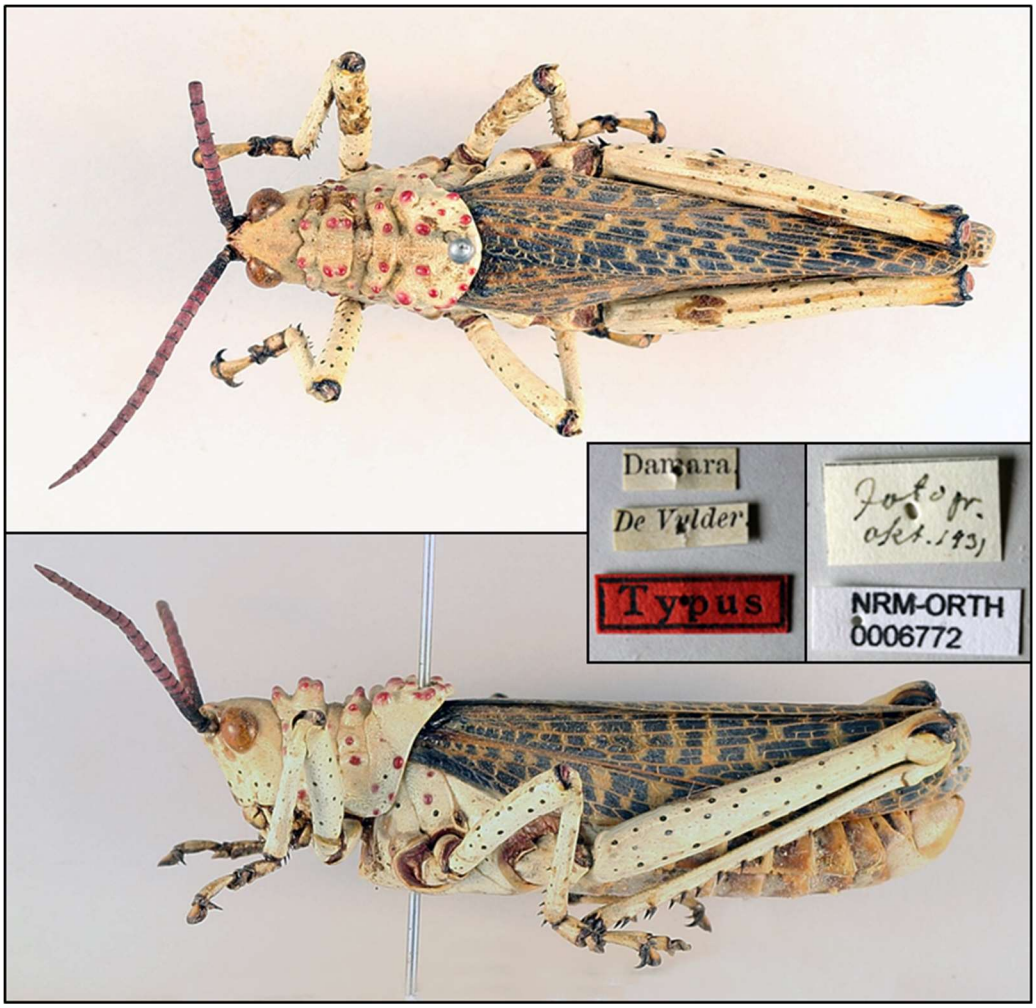

Figure 2.30. *Phymateus baccatus* Stål, 1876 (♂, HT) Namibia (NHRS).

2.3.2.10 Museum of Uppsala University (UZIU), Sweden

This museum holds more than 2 million insect specimens. For Orthoptera there are 119 taxa (both valid and synonyms) deposited here. Seventeen of them are from C. Linnaeus (1707-1778) and 98 of them are from C.P. Thunberg (1743-1828). Wallin (2001) and Wallin & Wallin (2001) treated with detail both Linnean and Thunberg types deposited at UZIU. For Pyrgomorphidae, there are 14 taxa with primary types. It was a pleasure to see that historical material and even more, it was in the original boxes (fig. 2.31). In figure 2.32, I selected some lateral views plus the labels of this historical material. Although few in number, due to its age, it required extra time to carefully took the images.

Figure 2.31. Original boxes used by Thunberg at UZIU.

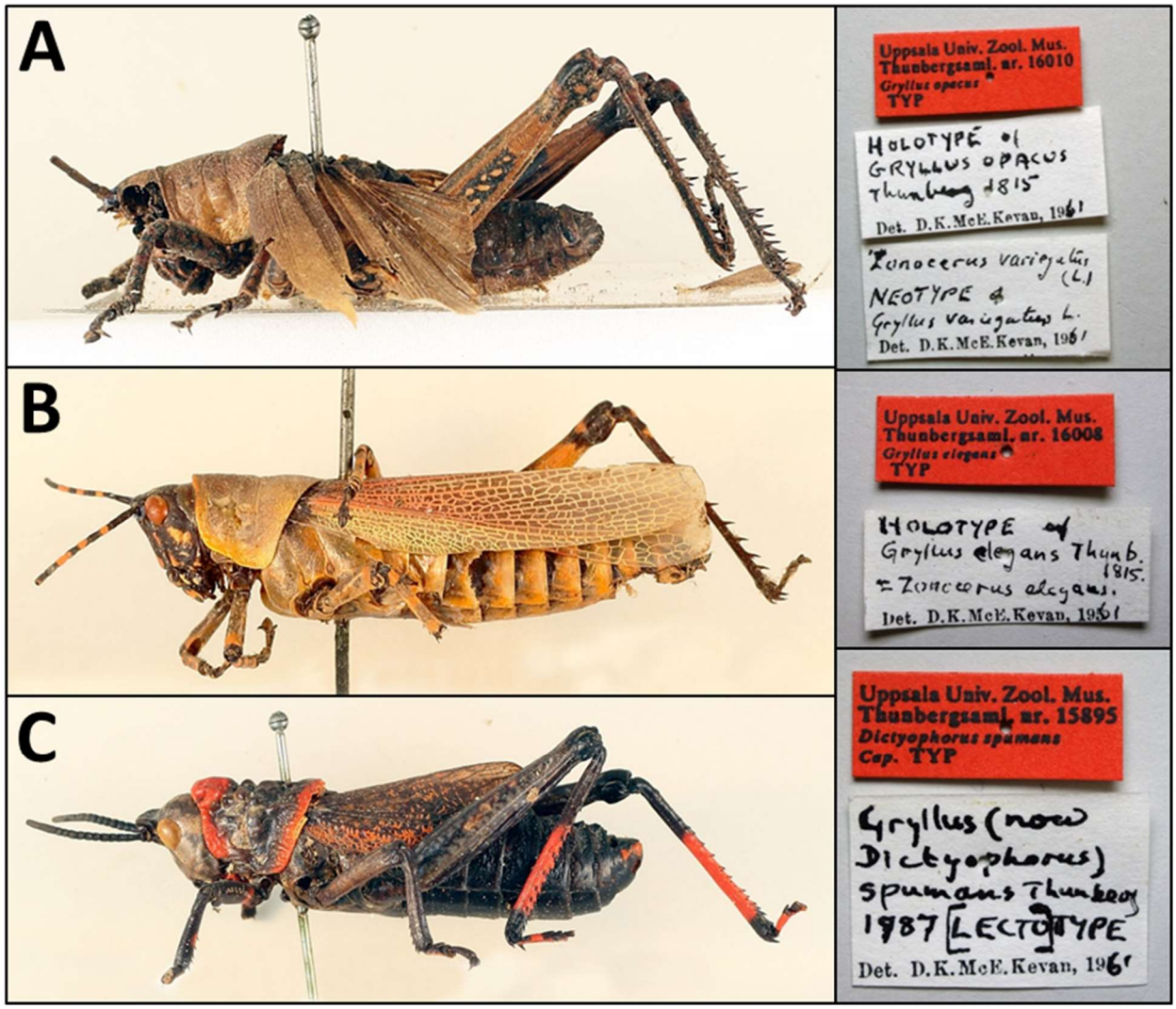

Figure 2.32. Pyrgomorphidae types from UZIU with their respective labels. **A.** *Zonocerus variegatus variegatus* (Linnaeus, 1758) (♂, NT) Africa; **B.** *Zonocerus elegans elegans* (Thunberg, 1815) (♂, HT) Africa; **C.** *Dictyophorus spumans spumans* (Thunberg, 1787) (♂, LT) South Africa.

2.3.2.11 Zoological Museum of the University of Copenhagen (ZMUC), Denmark

The entomological collection of this museum holds more than seven million specimens both pinned and in ethanol. There are about 10,500 primary types including near 8,000 types described by J.C. Fabricius (1745-1808). Concerning Orthoptera, there are 57 taxa (valid and synonyms) deposited here. For Pyrgomorphidae there are five species, mostly from Fabricius (fig. 2.33).

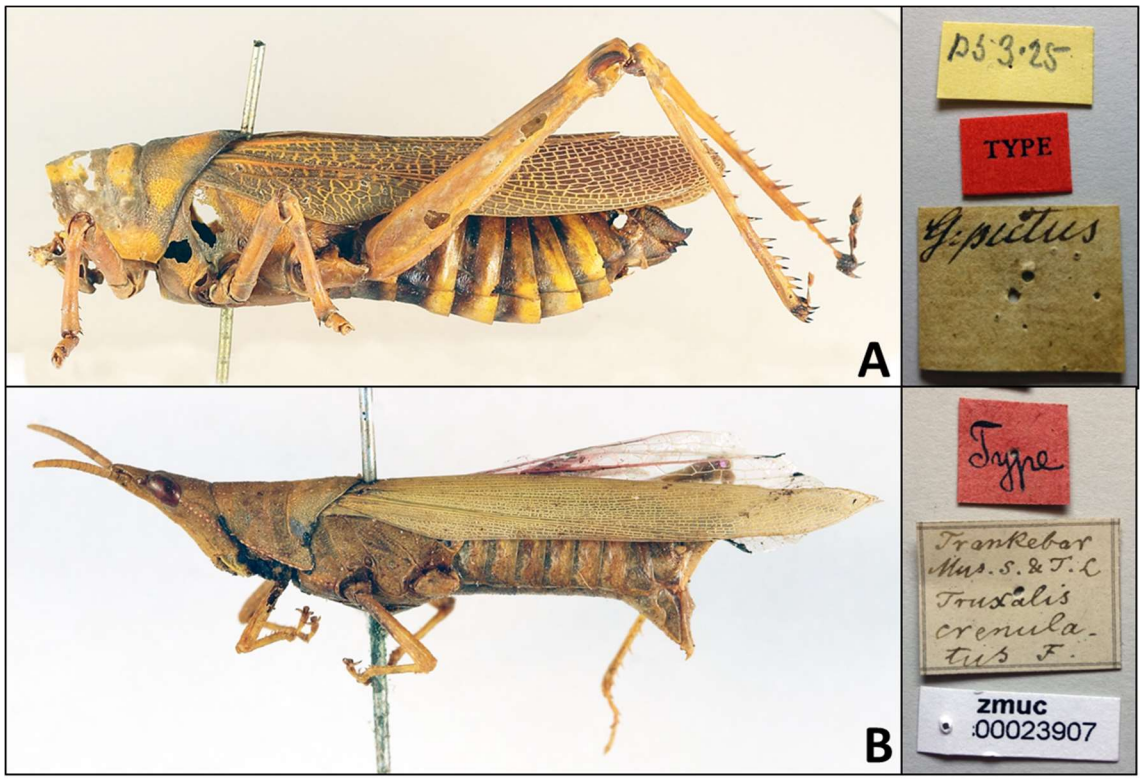

Figure 2.33. Pyrgomorphidae types from ZMUC with their respective labels. **A.** *Poekilocerus pictus* (Fabricius, 1775) (♀, HT) India; **B.** *Atractomorpha crenulata crenulata* (Fabricius, 1793) (♀, ST) India.

2.3.2.12 Museo Civico di Storia Naturale "Giacomo Doria" Genova, Italy

Founded in 1867, this entomological collection is worlwide in scope but with strong emphasis in Europe, Africa and Australasia. There are type material of 207 species of Orthoptera (173 valid and 34 synonyms) mainly due to the efforts of C. Brunner von Wattenwyl (1823-1914), L. Redtenbacher (1814-1876), Ignacio Bolívar y Urrutia (1850-1944), L. Chopard (1885-1971) and most recently by Baccio Baccetti (1931-2010) and Bruno Massa (1948-). Additionally the collection of B. Baccetti (19 valid species and 4 synonyms) is also housed here. For Pyrgomorphidae there are type material of 10 valid species, mainly from Bolívar (fig. 2.34).

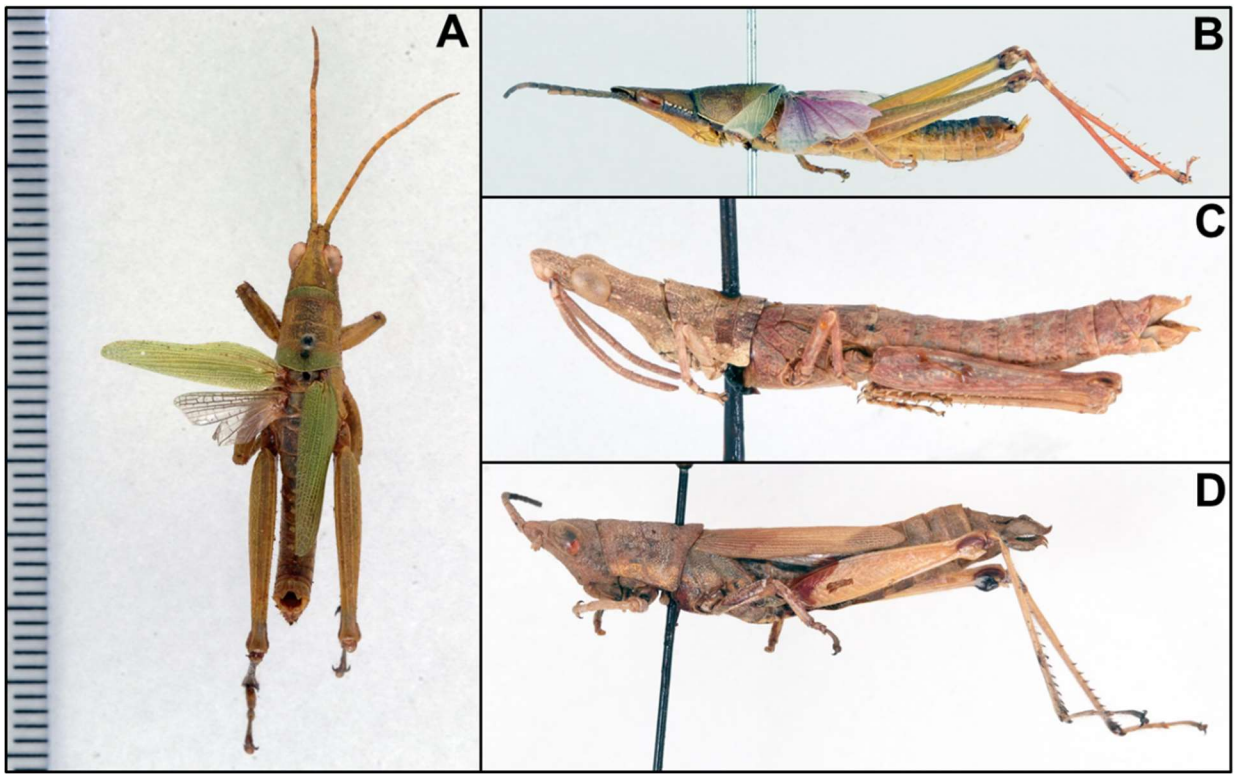

Figure 2.34. Pyrgomorphidae types from MCSN. **A.** *Chlorizeina unicolor unicolor* Brunner von Wattenwyl, 1893 (♂, ST) Myanmar; **B.** *Pseudomorphacris notata* (Brunner von Wattenwyl, 1893) (♂, LT) Myanmar; **C.** *Megalopyrga monochroma* Baccetti, 1985 (♀, HT) Somalia; **D.** *Mitricephala vittata* Bolívar, 1898 (♀, HT) Indonesia.

CHAPTER III

ILLUSTRATED KEYS TO PYRGOMORPHIDAE GENERA OF THE WORLD

3.1 Introduction

Currently with 149 genera, Pyrgomorphidae is widely distributed in the world. It is highly diverse in the Old Word (136 genera, 446 species) with some representatives in the New World (13 genera, 41 species).

Despite its worldwide distribution, only few genera truly show wide distribution. Because there is a high degree of endemicity at the genus level, I have created 12 regional keys that reflect these endemic biotas (fig. 3.1). For instance, the Africa key excludes Madagascar because this island has its own unique fauna (15/19 genera are endemic) and it is treated in a separate key, but it does include Socotra Island (part of the Arabian Peninsula country Yemen) because its biological affinities are African. At the beginning of each key, I define the included areas in order to facilitate to the user which key is the most adequate to use.

To increase the utility of the keys, I provide as much information as possible about the current distribution of the genus, as well as the number and names of valid species found in the region. There are 70 monotypic genera but I decided to use only the genus name in the keys because it is possible that new species can be added in the future. An asterisk next to genus name indicates that the genus is endemic to that region and is not going to be found in any other keys. Arrows in the images indicate the most important diagnostic characters mentioned in the key. The majority of the keys are based on male external morphology, unless specified otherwise. One exception is found in the couplet in the Indian subcontinent key composed of the genera *Orthacris* and *Neorthacris*, which will require examination of

male internal genialia. For the great majority of cases, I present a lateral view of a well-preserved specimen, although, in some cases, I also present females or lateral and dorsal views to show certain characteristics. I try to minimize the use of color as a diagnostic character because it is highly variable depending on collecting and preservation methods used. Most images used in these keys were photographs at the Song Laboratory of Insect Systematics and Evolution at Texas A&M University using the Visionary Digital imaging system equipped with a Canon EOS 6D DSLR camera, combined with a 100mm/65mm macro lens to take multiple images at different focal lengths. The resulting files were converted from RAW to TIFF format using Adobe Lightroom (v.4.4), stacked into a single composite image using Zerene Stacker (v.1.04), and then Adobe Photoshop CS6 Extended was used to add a scale bar and adjust light levels, background coloration, and sharpness as needed. For some genera, I was not able to obtain specimens and I present images of type material taken from various museums. Finally, I have also included specimens imaged by colleagues (Hojun Song and Bert Foquet) and only in three cases, no image is presented.

Some available keys were obsolete and published in different languages, such as French, Spanish, Portuguese and Chinese. I translated and modified them by adding new genera described after their publications. For other keys that were already in English, I updated and modified according to new nomenclatural arrangements. In some cases, the information to identify genera was not presented in the form of a key, and therefore, I converted into contrasting characteristics adequate to be used in dichotomous keys.

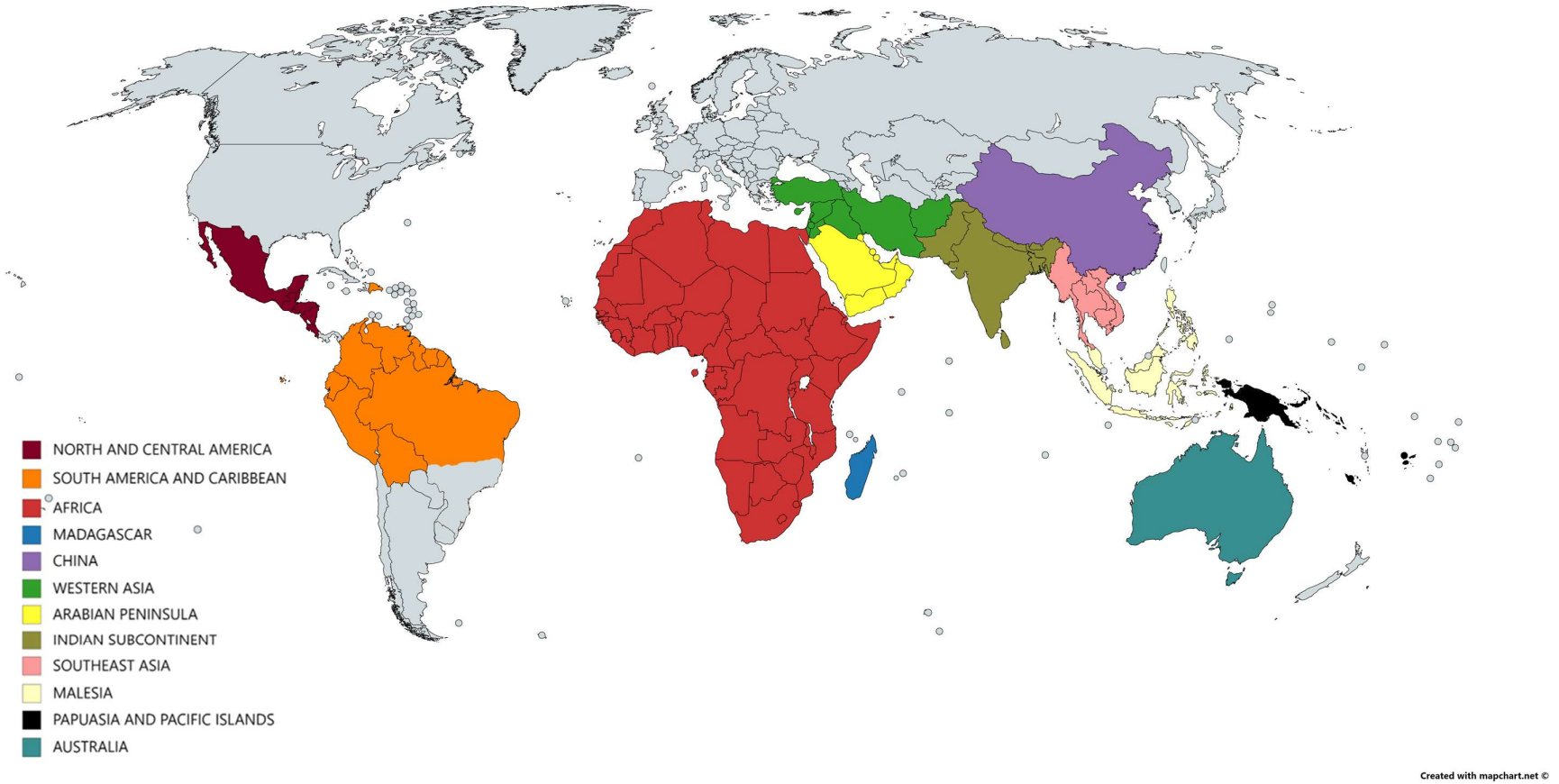

Figure 3.1. The twelve regions used in the respective keys. Created with mapchart.net ©.

3.2 Regional keys

3.2.1 Key to Pyrgomorphidae genera of North and Central America

Modified from Kevan et al. (1964).

Nine genera, all of them endemic to the area.

1. Overall body robust, strongly fusiform; mesosternal interspace strongly transverse (fig. 3.2B) 2

1'. Overall body cylindrical to weakly fusiform and rather slender to strongly elongate; mesosternal interspace not or not strongly transverse (fig. 3.2A) 3

2. Fastigium of vertex considerably longer than its width and rather acute (fig. 3.3B); posterior margin of pronotal disc strongly sinuous and emarginated; tegmina vestigial and tongue-like (fig. 3.3A), distinctly widening towards the base. (Guatemala to Costa Rica)…….***Prosphena**** **(1 sp.)**

(*P. scudderi*)

2'. Fastigium of vertex not much longer and often shorter than its width (fig. 3.3D; posterior margin of pronotal disc not strongly sinuous; tegmina vestigial and spatulate, narrowing towards the base (fig. 3.3C). (Mexico and Guatemala) .....…….***Sphenarium**** **(17 spp.)**

(*S. adelinae, S. borrei, S. crypticum, S. histrio, S. infernalis, S. macrophallicum, S.mexicanum, S. mínimum, S. miztecum, S. occidentalis, S. planum, S. purpurascens, S. rugosum, S. tarascum, S. totonacum, S. variabile, S. zapotecum*)

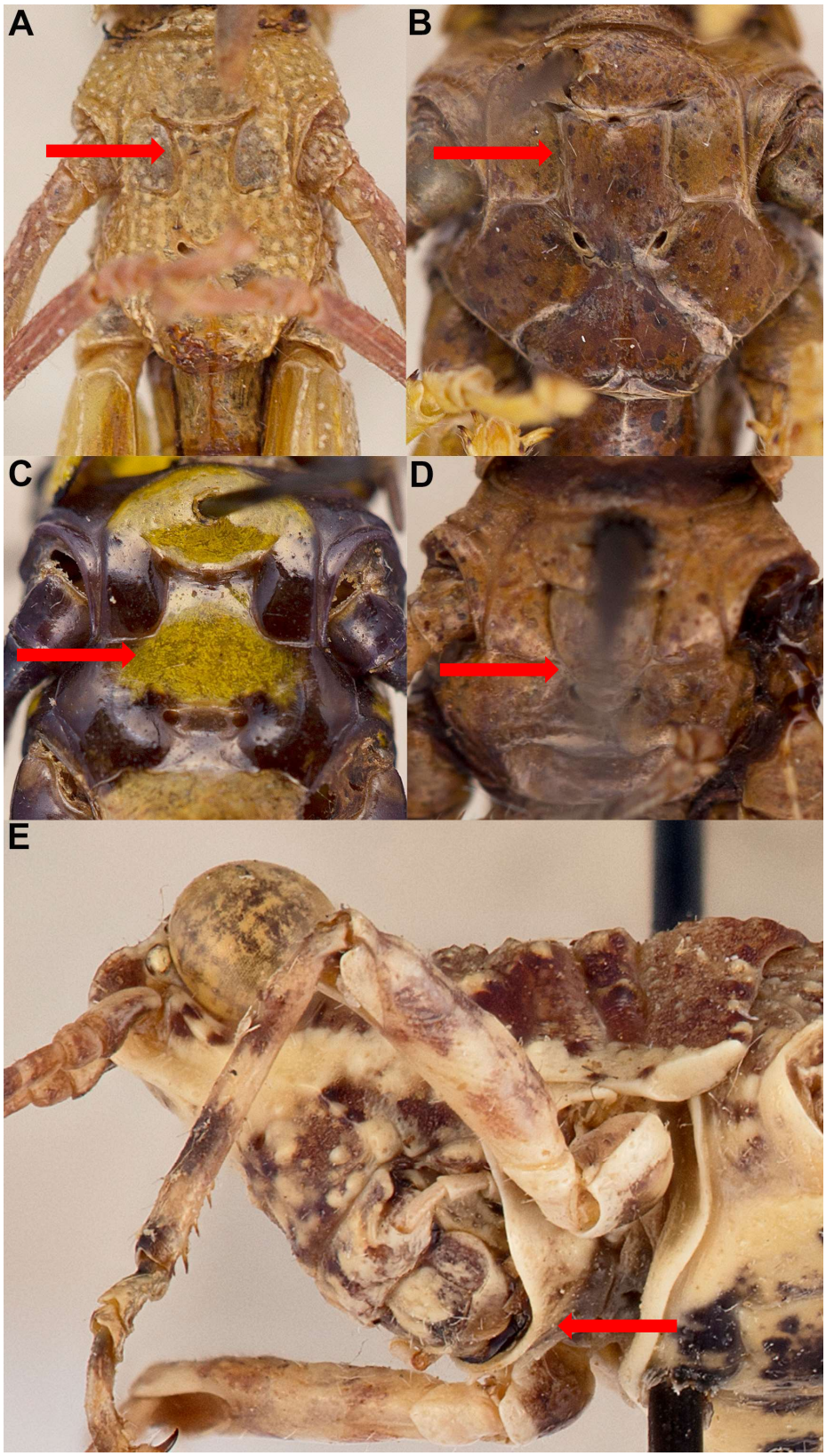

Figure 3.2. Ventral view of some Pyrgomorphidae. **A.** *Sphenacris crassicornis*. **B.** *Sphenarium histrio*. **C.** *Taphronota ferruginea*. **D.** *Phymella capensis*. **E.** *Chrotogonus oxypterus*.

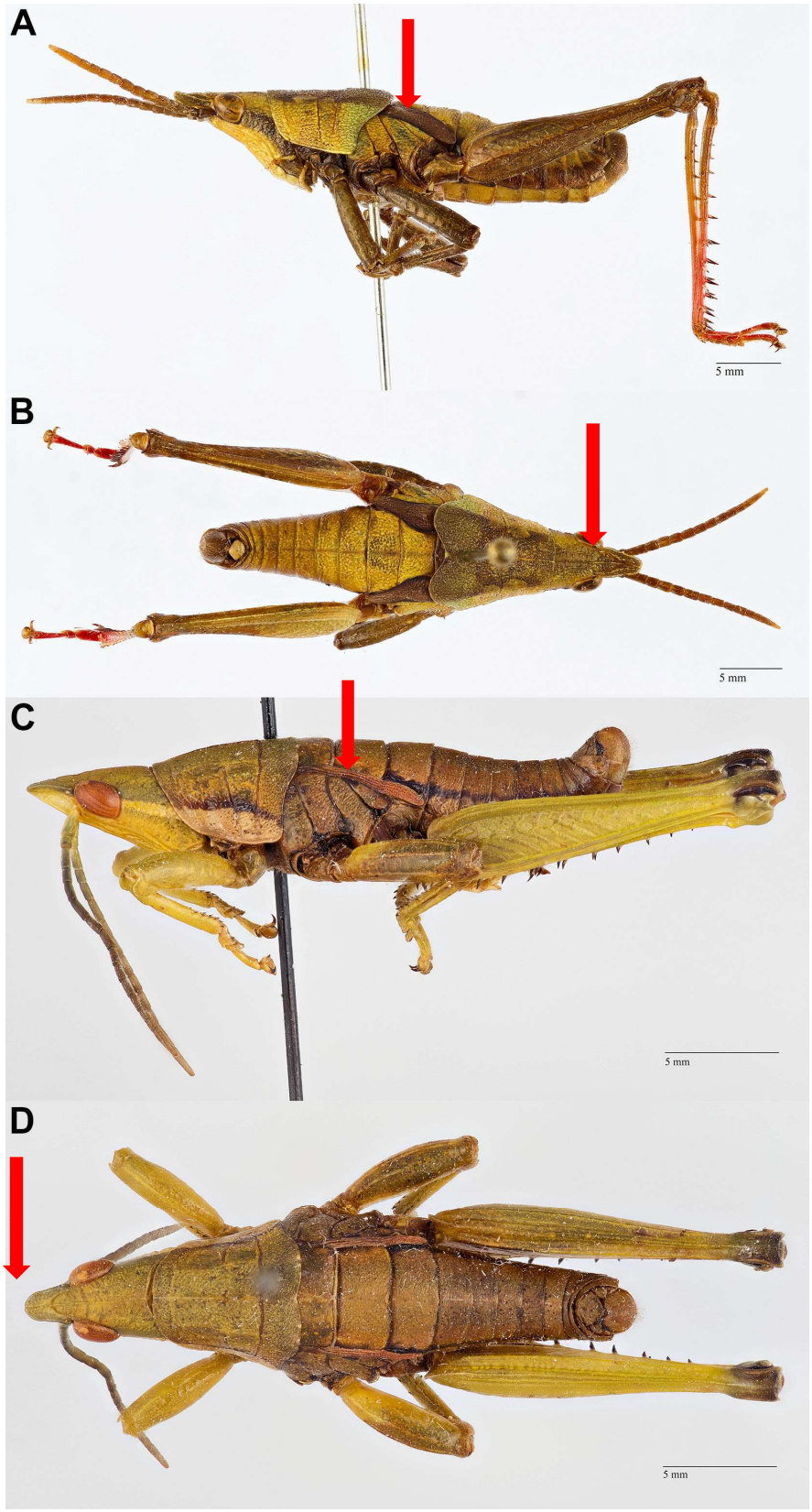

Figure 3.3. North and Central America Pyrgomorphidae 1. **A.** *Prosphena scudderi* male lateral view. **B.** *P. scudderi* male dorsal view. **C.** *Sphenarium histrio* male lateral view. **D.** *S. histrio* male dorsal view.

3. Body smooth, at most with a few isolated and scattered tubercles in the pronotum; apterous. ……4

3’. Body rugose, longitudinally striated or with numerous small granular tubercles; micropterous or apterous. ……..…….7

4. Body cylindrical (less so in females); males with 10th abdominal tergum modified into a large, blunt process covering all or part of epiproct (fig. 3.4A,C); females with ovipositor valves long, dorsal valves less than half as deep as the length from its widest point to the apex. .....……...……..5

4’. Body cylindrical or somewhat fusiform; males with 10th abdominal tergum unspecialized as above (fig. 3.5A); females with ovipositor valve shorter, dorsal valves more than half as deep as the length from its widest point to apex. ...…….…..6

5. Head with frontal profile oblique (frontal angle less than 40°); males with cerci stouter, blunt apically and as long as (or only slightly shorter) than the posterior prolongation of 10th abdominal tergum (fig. 3.4A); females with postero-lateral margins of the 8th abdomen sternum modified into posteriorly directed, acutely angular processes (fig. 3.4B). (Central and Southern Mexico) …..….....….***Ichthyotettix**** **(3 spp.)**

(*I. inexpectatus, I. mexicanus, I. stricticaudatus*)

5’. Head with frontal profile oblique (frontal angle at least 40°); males with cerci slender, pointed apically and much shorter than the posterior prolongation of 10th abdominal tergum (fig. 3.4C); females with postero-lateral margins of the 8th abdominal sternum not produced as above (fig. 3.4D). (Southern Mexico) ……..…***Piscacris**** **(2 spp.)**

(*P. affinis, P. robertsi*)

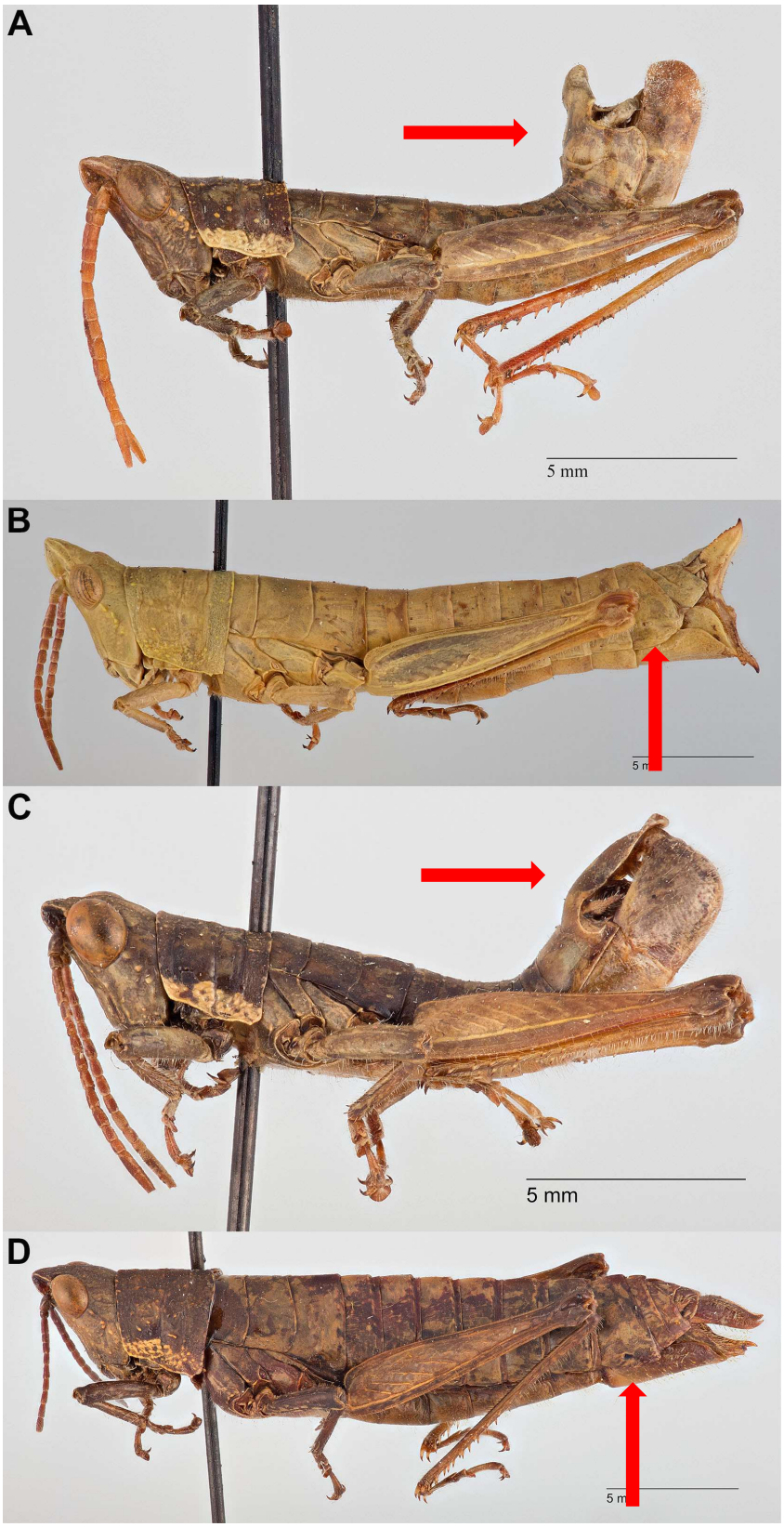

Figure 3.4. North and Central America Pyrgomorphidae 2. **A.** *Ichthyotettix mexicanus* male lateral view. **B.** *I. mexicanus* female lateral view. **C.** *Piscacris robertsi* male lateral view. **D.** *P. robertsi* female lateral view.

6. Body subfusiform (especially in females) (fig. 3.5B); Head with frontal profile oblique (frontal angle less than 40°); fastigium of vertex parabolic, not as broad as its length; mesosternal interspace about as wide as the mesosternal lobe (males) or wider (females). (Central Mexico) ……..……..…..***Sphenotettix**** **(1 sp.)**

(*S. nobilis*)

6’. Body cylindrical (fig. 3.5C,D). Head with frontal profile oblique (frontal angle much more than 40°); Fastigium of vertex triangular, slightly broader than its length; mesosternal interspace narrower than the mesosternal lobe. (Central and Southern Mexico)…….…….……..…….***Pyrgotettix**** **(1 sp.)**

(*P. pueblensis*)

7. Granular and tuberculate all over the body (figs. 3.6C & 3.7A)…….....……..8

7’. Not profusely granular; micropterous or apterous (fig. 3.6A,B). (Northwestern Mexico) ……***Ichthiacris**** **(8 spp.)**

(*I. aptera, I. californica, I. celata, I. costulata, I. elongata, I. parva, I. rehni, I. spinifera*)

8. With vestigial tegmina (fig. 3.6C,D). (West Central Mexico) ……..…...***Calamacris**** **(1 sp.)**

(*C. clendoni*)

8’. Apterous (fig. 3.7A,B). (East Central Mexico) …….…..…….***Sphenacris**** **(1 sp.)**

(*S. crassicornis*)

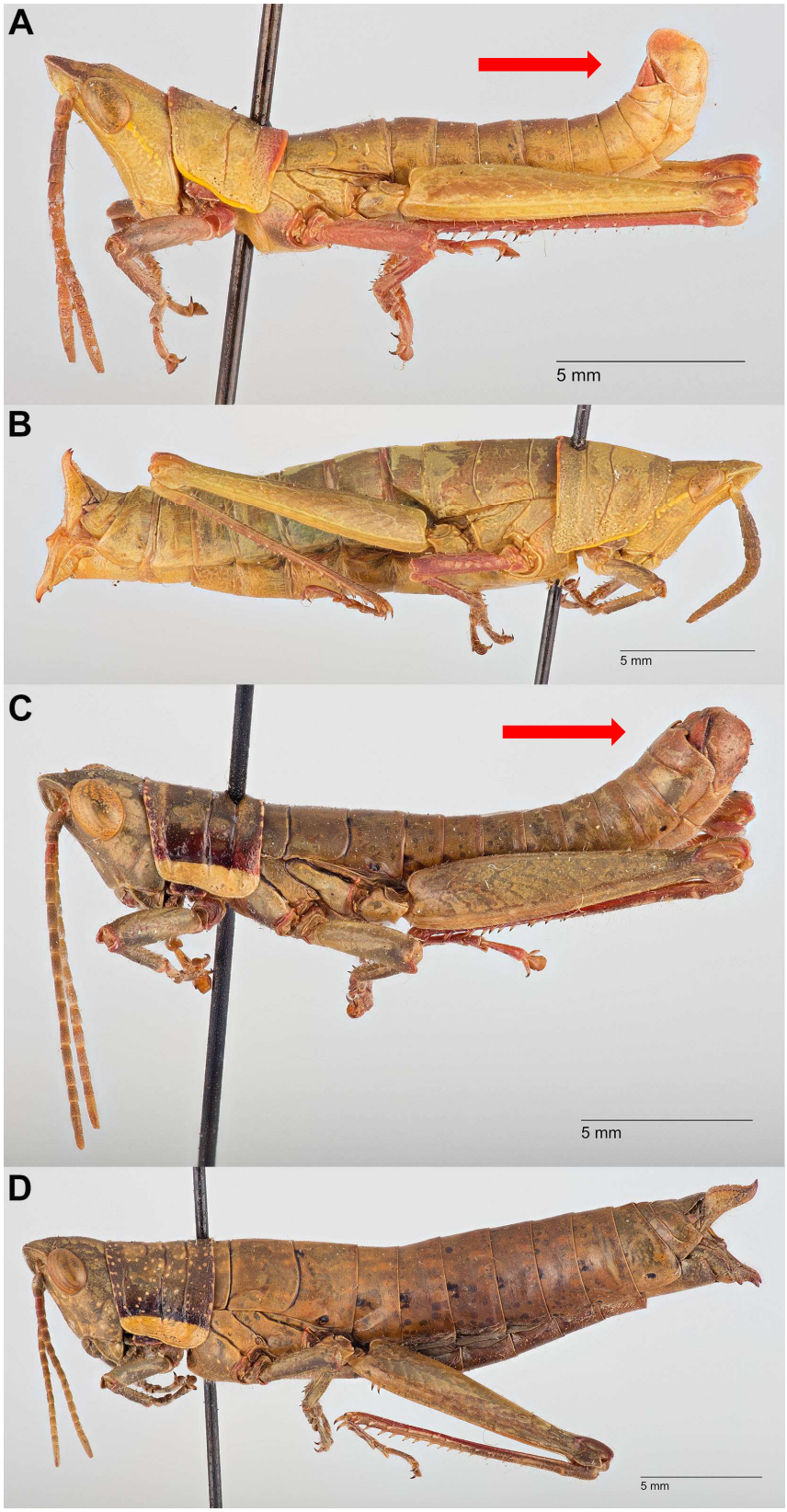

Figure 3.5. North and Central America Pyrgomorphidae 3. **A.** *Sphenotettix nobilis* male lateral view **B.** *S. nobilis* female lateral view **C.** *Pyrgotettix pueblensis* male lateral view **D.** *P. pueblensis* female lateral view.

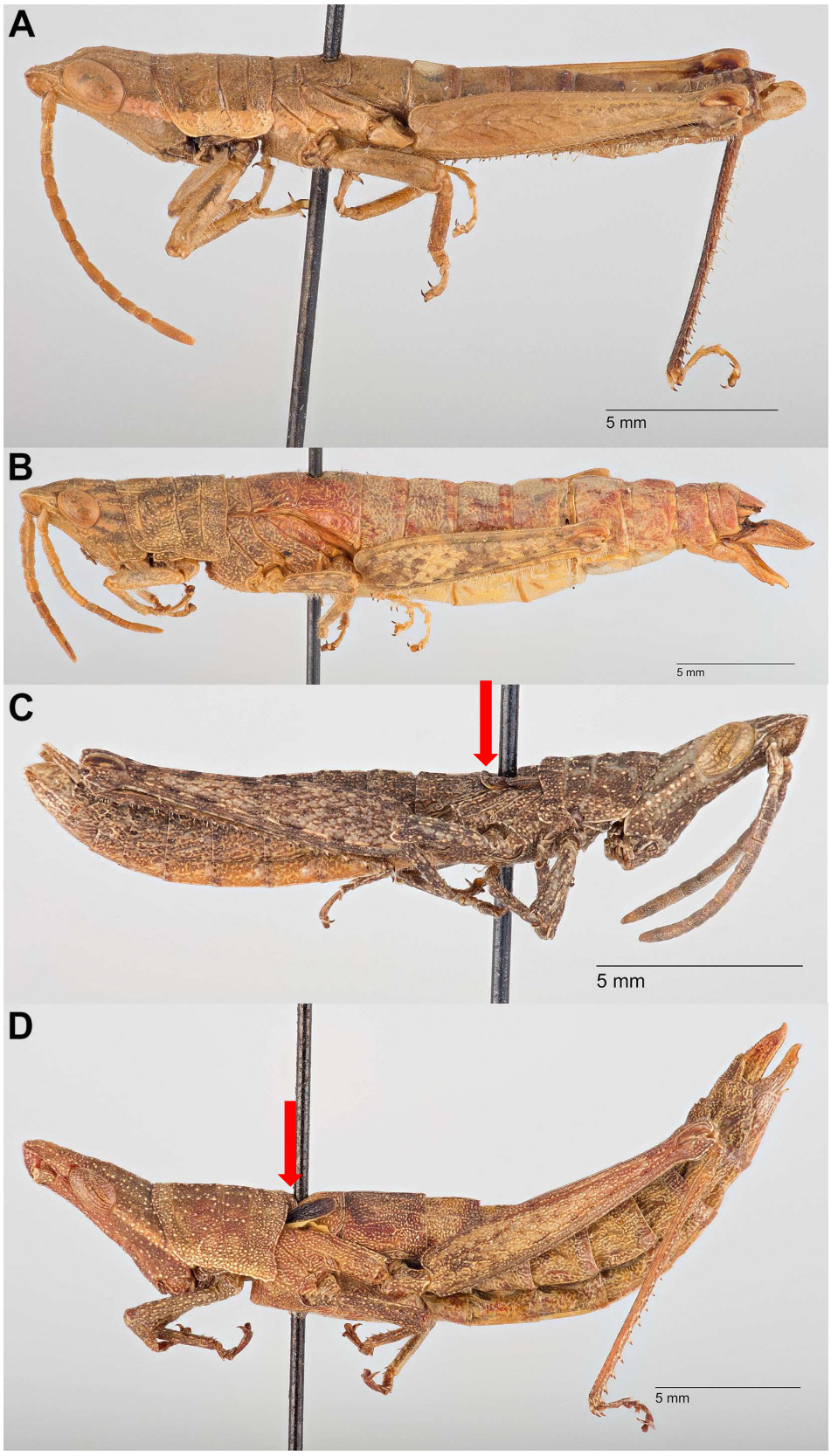

Figure 3.6. North and Central America Pyrgomorphidae 4. **A.** *Ichthiacris aptera* male lateral view. **B.** *I. aptera* female lateral view. **C.** *Calamacris clendoni* male lateral view. **D.** *C. clendoni* female lateral view.

Figure 3.7. North and Central America Pyrgomorphidae 5. **A.** *Sphenacris crassicornis* male lateral view. **B.** *S. crassicornis* female lateral view.

3.2.2 Key to Pyrgomorphidae genera of South America and the Caribbean

Based on information from Alves Dos Santos (2005) and Perez Gelabert et al. (1995).

Four genera, all endemic to this region.

1. Apterous. ……...2

1'. Fully winged or micropterous. …….……3

2. Irregular integument; lower marginal area of hind femur approximately as wide as medial area (fig. 3.8A,B); (East and central upper half of South America) .....***Omura**** **(1 sp.)**

(*O. congrua*)

2'. Striated and tuberculate integument through the body; lower marginal area of hind femur narrower than medial area (fig. 3.8C,D). (Eastern Brazil) …….....***Algete**** **(1 sp.)**

(*A. brunneri*)

3. Fully winged, in some cases tegmina reduced but always passing third coxae (fig. 3.9A,B). (Colombia, Venezuela, Brazil [Goiás, Mato Grosso, Minas Gerais])…..***Minorissa**** **(2 spp.)**

(*M. pustulata, M. volxemi*)

3'. Vestigial tegmina, always smaller than eyes (fig. 3.9C,D). (Dominican Republic)

…….....……..***Jaragua**** **(2 spp.)**

(*J. oviedensis, J. serranus*)

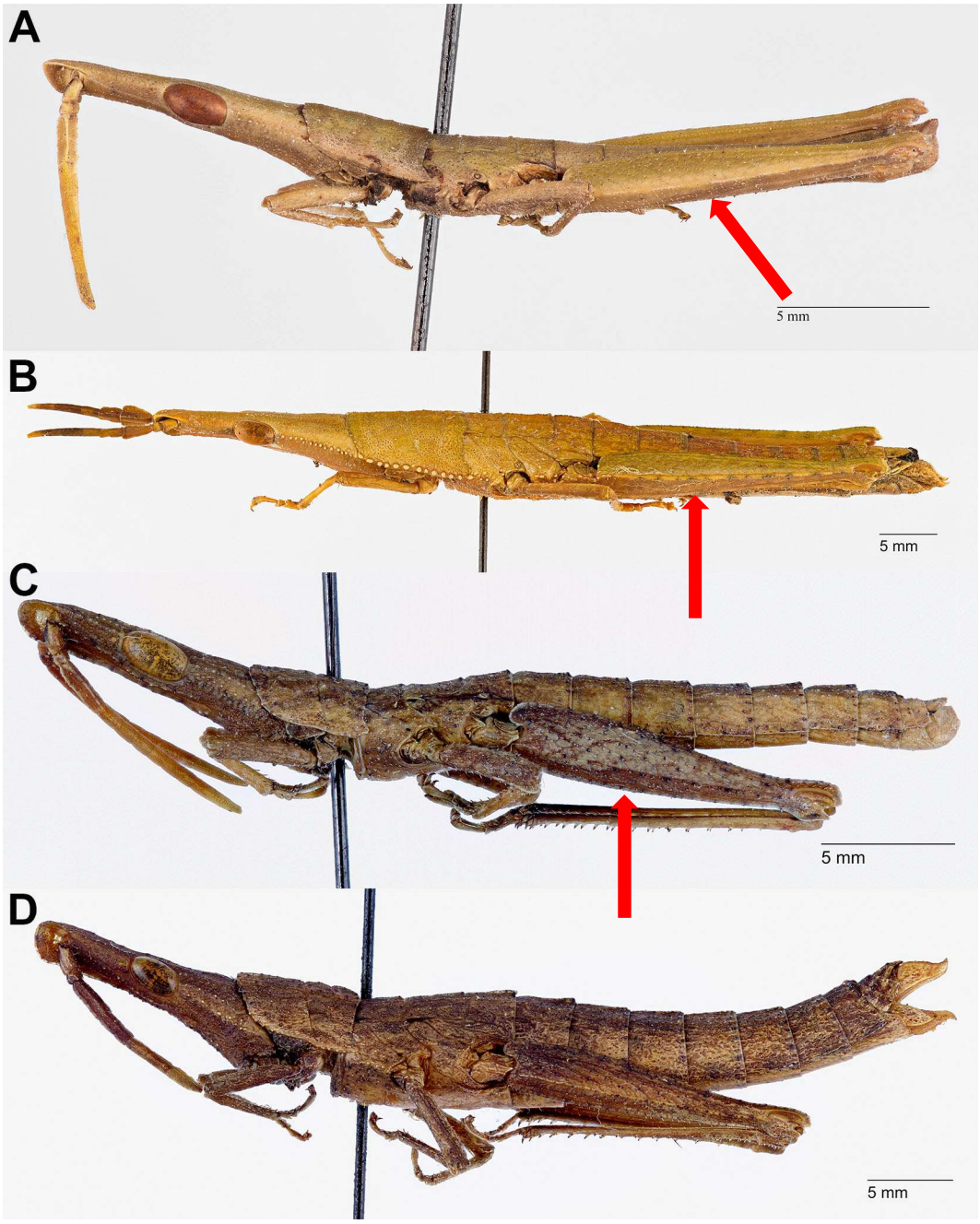

Figure 3.8. South America and Caribbean Pyrgomorphidae 1. **A.** *Omura congrua* male lateral view. **B.** *O. congrua* female lateral view. **C.** *Algete brunneri* male lateral view. **D.** *A. brunneri* female lateral view.

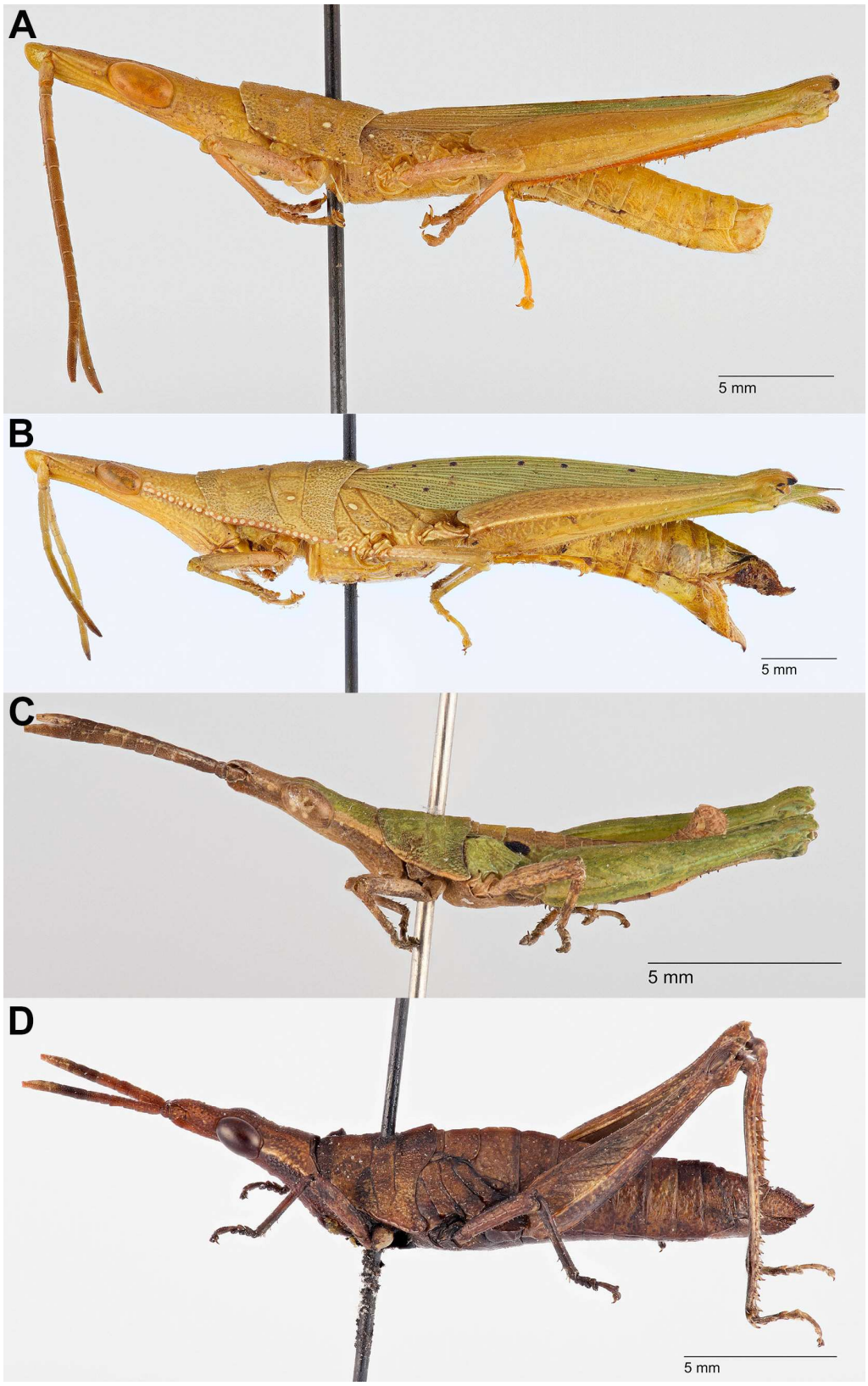

Figure 3.9. South America and Caribbean Pyrgomorphidae 2. **A.** *Minorissa pustulata* male lateral view. **B.** *M. pustulata* female lateral view. **C.** *Jaragua oviedensis* male lateral view. **D.** *J. oviedensis* female lateral view.

3.2.3 Key to Pyrgomorphidae genera of Africa (excluding Madagascar and including Socotra Island)

Modified from Dirsh (1965).

Fifty five genera, forty nine endemic to the region.

1. Antenna of variable shape, without strongly serrated edges, with well-separated basal segments of flagellum and with simple, not bilobate, apical segment. …….……2

1'. Antenna in cross section triangular, with strong irregularly serrated edges, fused basal segments (fig. 3.10A) and bilobate apex of apical segment. (São Tomé) .....***Geloiodes** (1 sp.)** (*G. cavifrons*)

2. Anterior margin of prosternum forming a wide collar, covering the posterior and lower part of the mouth (fig. 3.2E). ..……..……3

2'. Anterior margin of prosternum not covering the posterior and lower part of the mouth. …….……...7

3. Macropterous, brachypterous or micropterous; external spur of inner side of hind tibia as long as or shorter than internal one. ……..…….4

3'. Apterous; external spur of inner side of hind tibia longer than internal one. ……...6

4. Spurs of hind tibia longer than basal tarsal segment; middle femur thin and strongly elongated, as long as or longer than head and pronotum together (fig. 3.10B); lower basal lobe of hind femur shorter than upper one. (Upper half of Africa) …….....***Tenuitarsus* (2 spp.)** (*T. angustus, T. sudanicus*)

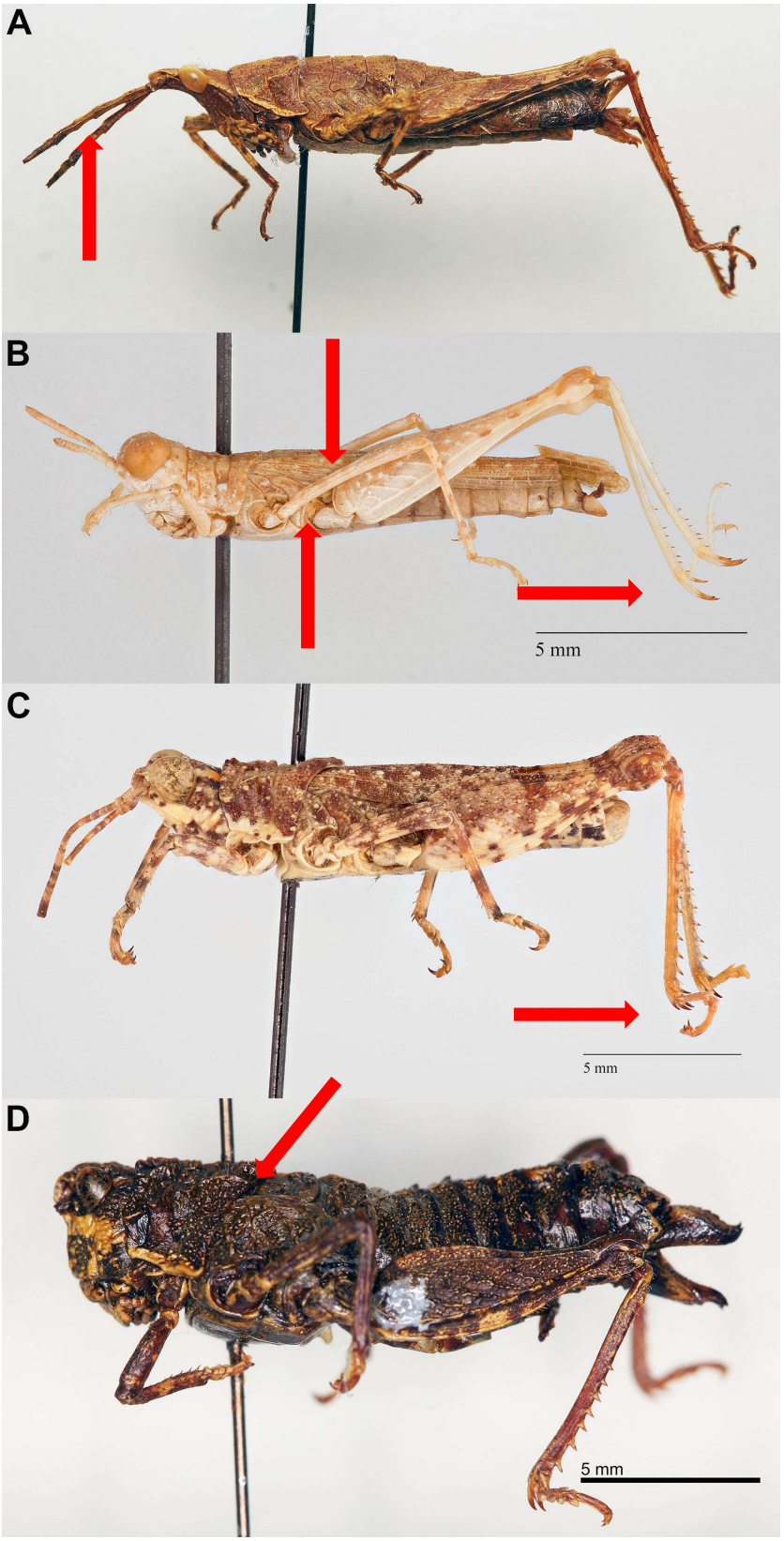

Figure 3.10. African Pyrgomorphidae 1. **A.** *Geloiodes cavifrons* female lateral view. **B.** *Tenuitarsus angustus* male lateral view. **C.** *Chrotogonus oxypterus* male lateral view. **D.** *Shoacris bormansi* female lateral view.

4’. Spurs of hind tibia shorter than basal tarsal segment; middle femur short, much shorter than head and pronotum together; lower basal lobe of hind femur longer than the upper one. ……....5

5. Tegmina and hind wings present (fig. 3.10C), protruding from under pronotum even when vestigial. (Throughout Africa) …….***Chrotogonus*** **(5 spp.)**

(*C. hemipterus, C. homalodemus, C. senegalensis, C. arenícola, C. tuberculatus*)

5’. Tegmina vestigial, covered by pronotum (fig. 3.10D). (Ethiopia) ……....***Shoacris**** **(1 sp.)**

(*S. bormansi*)

6. Meso- and metasternal interspaces close to one another, separated by suture; fastigium of vertex elongated (fig. 3.11A), apical fastigial areolae with well-developed marginal carinulae. (Angola) ……..……..…….***Caconda**** **(2 spp.)**

(*C. burri, C. fusca*)

6’. Meso- and metasternal interspaces partly fused; fastigium of vertex short (fig. 3.11B), apical fastigial areolae without posterior marginal carinulae. (Angola) ……..***Stibarosterna**** **(1 sp.)**

(*S. serrata*)

7. Antennal bases located in front of lateral ocelli. …….……...……...8

7’. Antennal bases below and behind lateral ocelli. …….……...11

8. Vestigial tegmina or apterous. …….……..9

8’. Fully winged (fig. 3.11C). (Sub-Saharan Africa) ……..……***Atractomorpha*** **(5 spp.)**

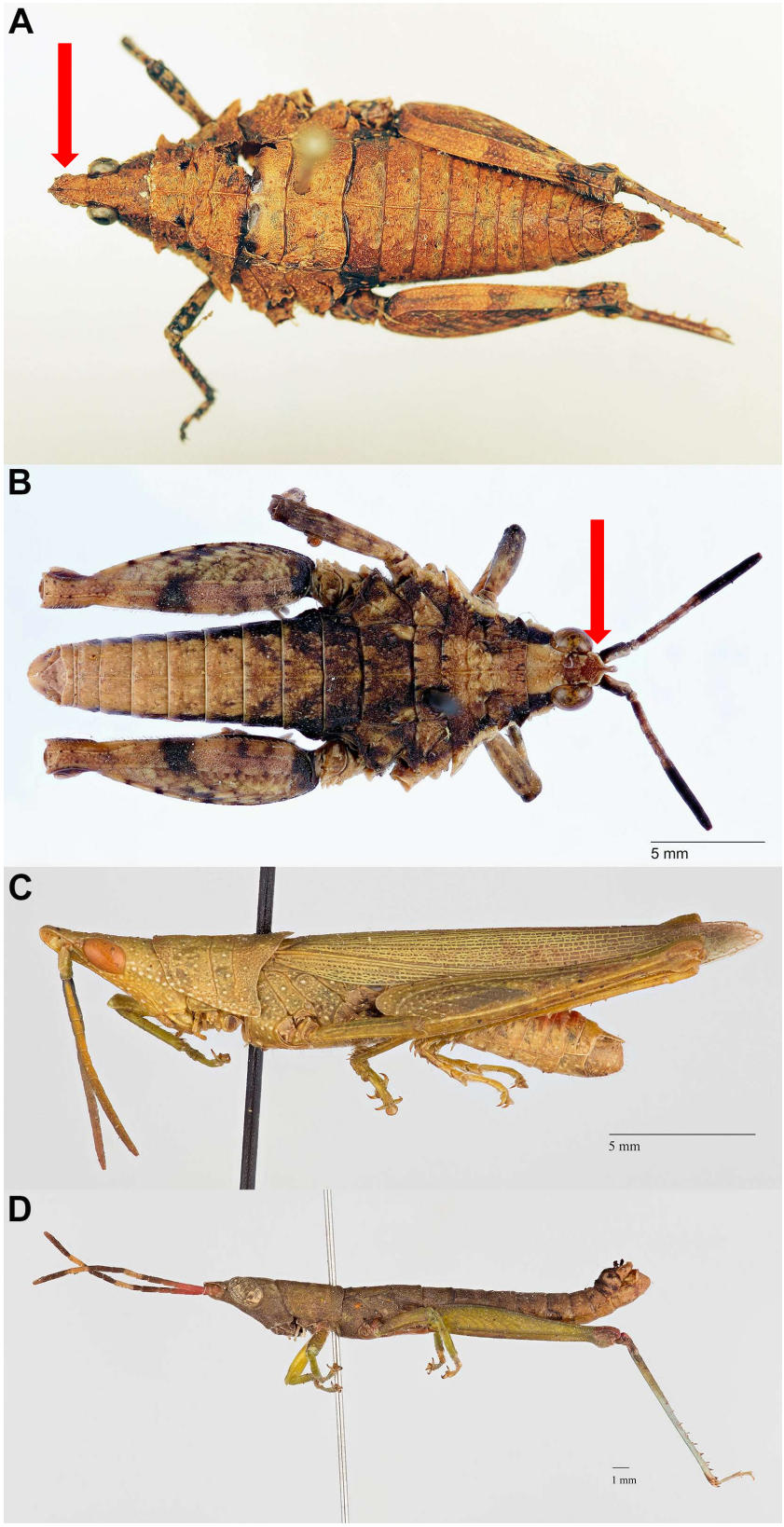

Figure 3.11. African Pyrgomorphidae 2. **A.** *Caconda burri* female dorsal view. **B.** *Stibarosterna serrata* male dorsal view. **C.** *Atractomorpha aberrans* male lateral view. **D.** *Chapmanacris sylvatica* male lateral view.

(*A. aberrans, A. acutipennis, A. occidentalis, A. orientalis, A. rufopunctata*)

9. Apterous. ……10

9’. Vestigial tegmina (fig. 3.11D). (Ghana) ……..……***Chapmanacris**** **(1 sp.)**

(*C. sylvatica*)

10. In lateral view, length of the space between eye and anterior margin of pronotum longer than the length of the eye (fig. 3.12A). (Somalia) …….....***Megalopyrga**** **(1 sp.)**

(*M. monochroma*)

10’. In lateral view, length of the space between eye and anterior margin of pronotum shorter than the length of the eye (fig. 3.12B). (Socotra Island) .....***Xenephias**** **(1 sp.)**

(*X. socotranus*)

11. Dorsum and lateral margins of pronotum with large teeth, tubercles or large granules. ……..12

11’. Dorsum and lateral margins of pronotum smooth, granulose or with small tubercles and ridges. ……...……...17

12. Mesosternal interspace distant from metasternal one (fig. 3.2C). ……...…….13

12’. Mesosternal interspace close to metasternal, separated by suture only (fig. 3.2D & 3.12C). (South Africa) ……...…….....……***Phymella**** **(1 sp.)**

(*P. capensis*)

13. Lateral margins of dorsum of pronotum, particularly in prozona, with large, obtuse, or subacute teeth and tubercles, or granulose. …….……14

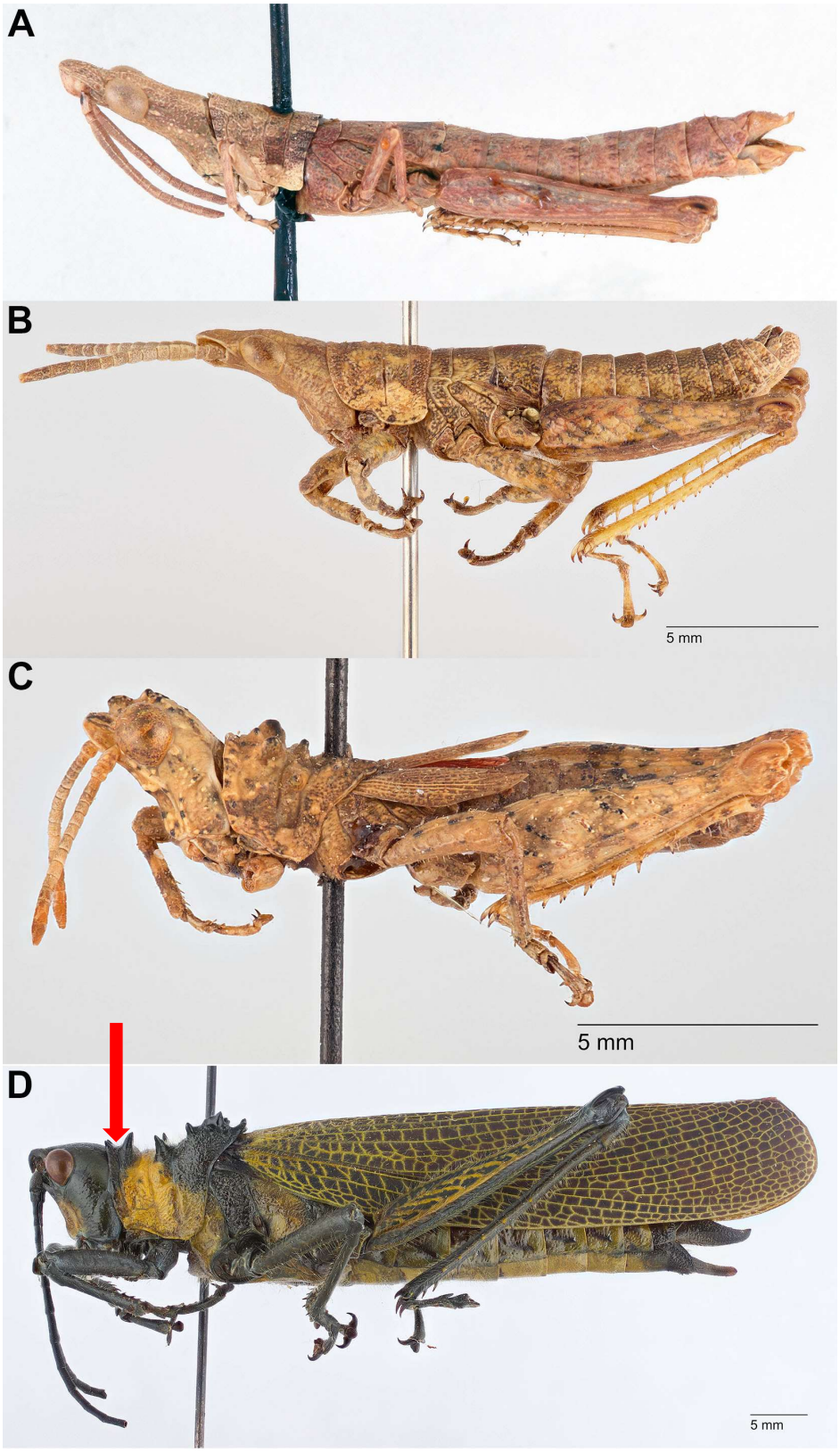

Figure 3.12. African Pyrgomorphidae 3. **A.** *Megalopyrga monochroma* female lateral view. **B.** *Xenephias socotranus* male lateral view. **C.** *Phymella capensis* male lateral view. **D.** *Rutidoderes cinctus* female lateral view.

13’. Lateral margins of dorsum of pronotum with acute teeth-like spines (fig. 3.12D). (West, Central and East Africa) ……..…….……***Rutidoderes**** **(3 spp.)**

(*R. cinctus, R. concolor, R. squarrosus*)

14. Entire dorsum of pronotum covered with obtuse or subacute teeth and tubercles. ..15

14’. Entire dorsum of pronotum strongly granulose (fig. 3.13A). (Sub-Saharan Africa)

……...……***Taphronota**** **(8 spp.)**

(*T. cacuminata, T. stali, T. calliparea, T. ferruginea, T. grandis, T. merceti, T. occidentalis, T. verrucosa*)

15. Fully winged. …….……16

15’. Tegmina highly reduced (fig. 3.13B). (Somalia) ….....….***Paraphymateus**** **(1 sp.)**

(*P. roffeyi*)

16. Hind wings with tessellated pattern and darker spots (fig. 3.13C). (Sub-Saharan Africa) …….....…….……...***Phymateus*** **(10 spp.)**

(*P. baccatus, P. leprosus, P. aegrotus, P. bolivari, P. cinctus, P. iris, P. karschi, P. morbillosus, P. pulcherrimus, P. viridipes*)

16’. Hind wings without tessellated pattern, blending into green at tip or anteriorly (3.14A). (Sub-Saharan Africa) ……..……...……***Phyteumas**** **(3 spp.)**

(*P. olivaceus, P. purpurascens, P. whellani*)

17. Pronotum with low rounded tubercles, wrinkles and ridges, in front of the first sulcus with large median inflation; valves of ovipositor straight. ……..18

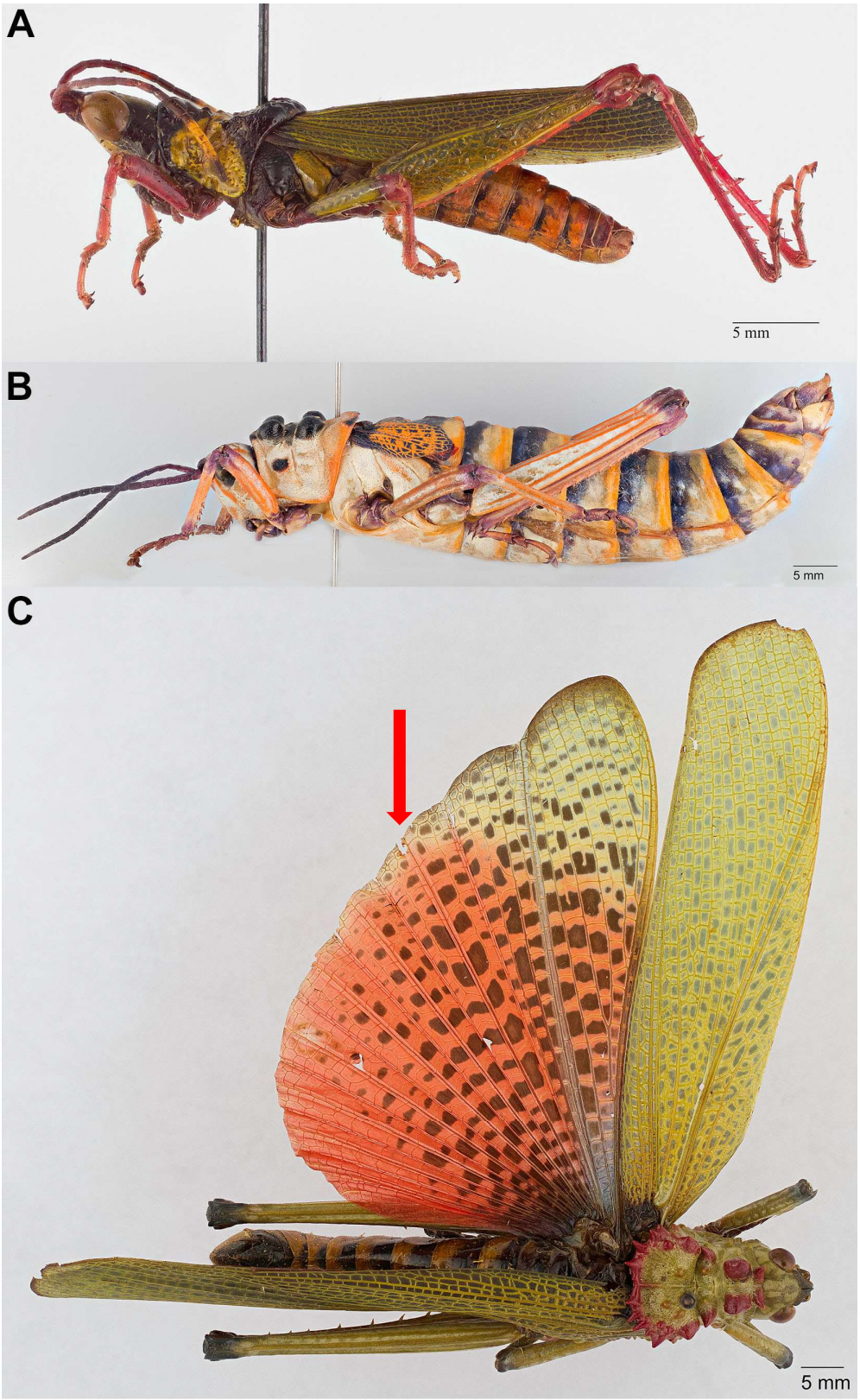

Figure 3.13. African Pyrgomorphidae 4. **A.** *Taphronota ferruginea* male lateral view. **B.** *Paraphymateus roffeyi* female lateral view. **C.** *Phymateus cinctus* male dorsal view.

17’. Pronotum smooth or finely granulose, if pronotum tuberculate then pyrgomorph size is small, without median inflation; valves of ovipositor curved. …..……..22

18. Median inflation in front of the first sulcus of pronotum low; entire pronotum covered with ridges and granules. ……...…..……19

18’. Median inflation in front of first the sulcus high; entire pronotum tuberculate. ……..20

19. Entire pronotum covered with thick, irregular, longitudinal ridges (fig. 3.14B), anterior and posterior margins slightly excised. (Western and Central Africa) .....***Camoensia**** **(1 sp.)**

(*C. insignis*)

19’. Entire pronotum roughly granulose (fig. 3.14C), anterior and posterior margins not excised. (Sub-Saharan Africa) …….…….……***Maura**** **(4 spp.)**

(*M. bolivari, M. lurida, M. marshalli, M. rubroornata*)

20. Hind tibia not widened; tegmina vestigial or shortened. …….……..21

20’. Hind tibia in apical half widened (fig. 3.14D); tegmina and hindwings fully developed or shortened. (Sub-Saharan Africa) …….....…..….***Dictyophorus**** **(4 spp.)**

(*D. cuisinieri, D. spumans, D. griseus, D. karschi*)

21. Tegmina vestigial or shortened. If shortened, cell size large (fig. 3.15A). (Nigeria, Cameroon, Gabon) ….....……...***Parapetasia**** **(1 sp.)**

(*P. femorata*)

21’. Tegmina shortened with cell size small (fig. 3.15B). (Tanzania) .***Loveridgacris**** **(1 sp.)**

(*L. impotens*)

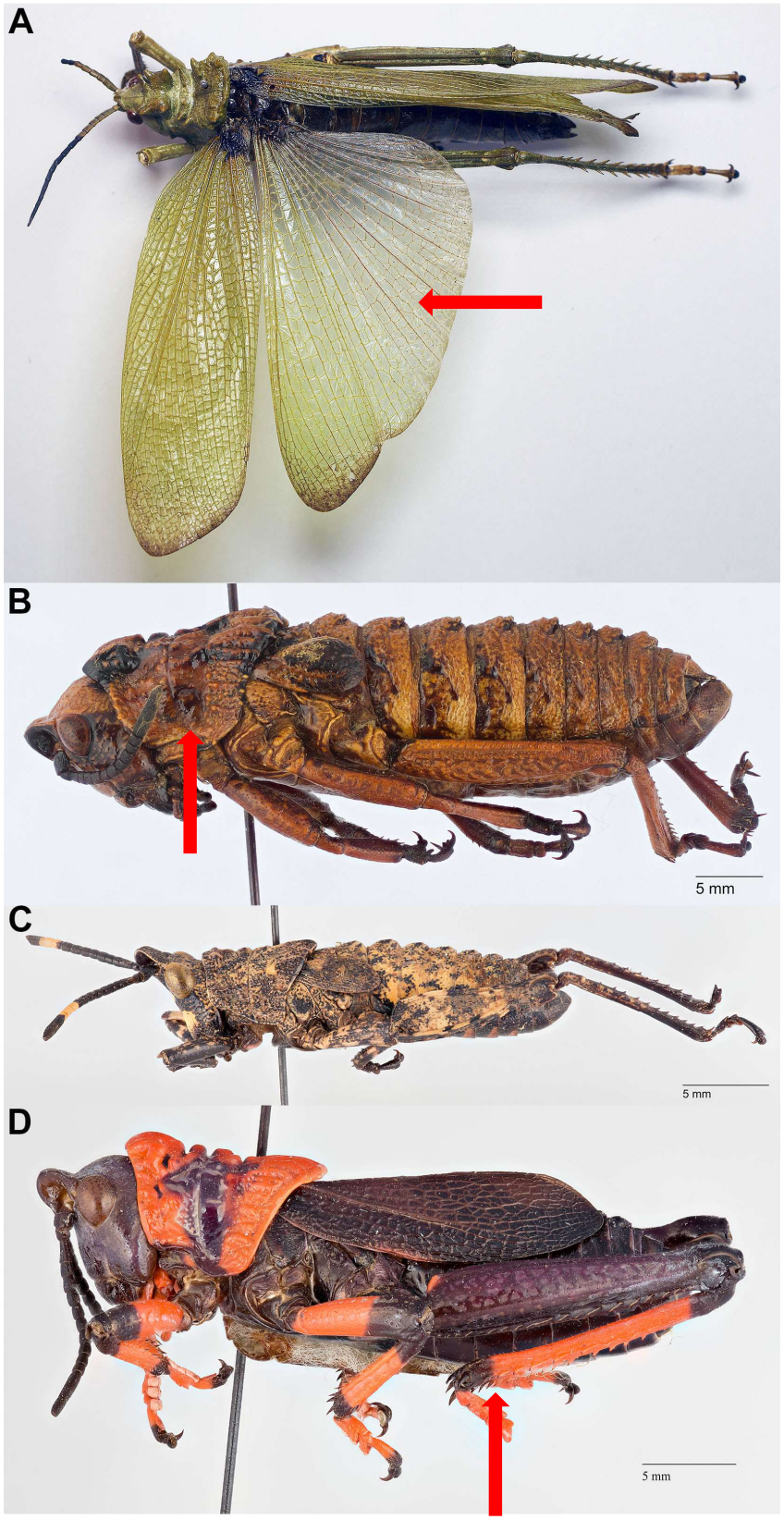

Figure 3.14. African Pyrgomorphidae 5. **A.** *Phyteumas olivaceus* female dorsal view. **B.** *Camoensia insignis* male lateral view. **C.** *Maura bolivari* male lateral view. **D.** *Dictyophorus spumans* male lateral view.

22. First abdominal tergite with glandular tubercle (fig. 3.15C); tegmina fully developed or shortened. …….....…….……23

22’. First abdominal tergite without glandular tubercle. …….……24

23. Tegmina fully developed or shortened and not overlapping at the base (fig. 3.15C). (Sub-Saharan Africa) …….....……...…….……..***Zonocerus*** **(2 spp.)**

(*Z. elegans, Z. variegatus*)

23’. Tegmina fully developed and overlapping at the base, but still showing the glandular tubercle (fig. 3.15D). (Socotra Island) …….....***Physemophorus**** **(1 sp.)**

(*P. sokotranus*)

24. Apterous or micropterous. 25

24’. Macropterous. 43

25. Apterous. 26

25’. Micropterous (not functional tegmina) or brachypterous (reduced but functional tegmina). 29

26. Hind femur comparatively wide, not reaching the tip of abdomen. 27

26’. Hind femur narrow and passing the tip of abdomen. 28

27. Dorsum of pronotum crossed by only one transverse sulcus (fig. 3.16A); mesosternal interspace inverse-triangular, mesosternal lobes almost connected. (Somalia).

……***Parorthacris**** **(1 sp.)**

(*P. somalica*)

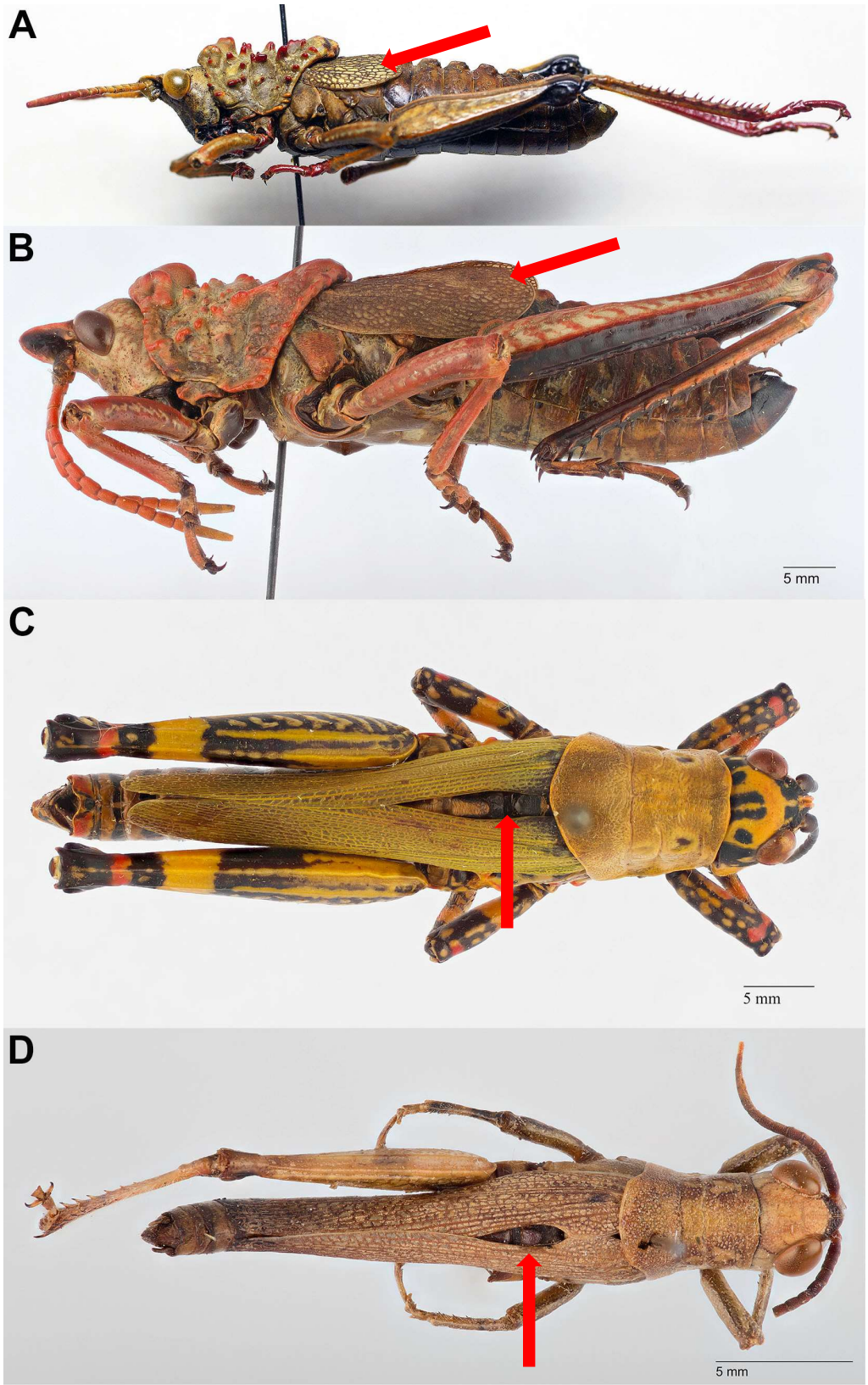

Figure 3.15. African Pyrgomorphidae 6. **A.** *Parapetasia femorata* male lateral view. **B.** *Loveridgacris impotens* male lateral view. **C.** *Zonocerus variegatus* male dorsal view. **D.** *Physemophorus sokotranus* male dorsal view.

27’. Dorsum of pronotum crossed by two transverse sulci (fig. 3.16B); mesosternal interspace square, mesosternal lobes far apart. (Somalia) .....***Vittisphena**** **(1 sp.)**

(*V. somalica*)

28. Fastigium of vertex acutely angular above (fig. 3.16C). (Central Africa)

.....***Occidentosphena**** **(2 spp.)**

(*O. ruandensis, O. uvarovi*)

28’. Fastigium of vertex parabolic above (fig. 3.16D). (Sudan, Uganda, Kenya, Tanzania)

……..…….……***Parasphena**** **(17 spp.)**

(*P. campestris, P. cheranganica, P. chyuluensis, P. elgonensis, P. hanangensis, P. imatongensis, P. kaburu, P. keniensis, P. kinangopa, P. kulalensis, P. mauensis, P. meruensis, P. nairobiensis, P. naivashensis, P. ngongensis, P. pulchripes, P. teitensis*)

29. Fastigium of vertex two or three times as long as its width. 30

29’. Fastigium of vertex as long as or shorter than or slightly longer than its width. 31

30. Fastigium of vertex about twice as long as its width (fig. 3.17A); tegmina narrow; integument strongly, regularly granulose. (Zimbabwe, Mozambique) .....***Chirindites**** **(1 sp.)**

(*C. odendaali*)

30’. Fastigium of vertex about three times as long as its width (fig. 3.17B); tegmina lobiform; integument smooth and shiny. (Tanzania) .....***Sphenexia**** **(1 sp.)**

(*S. fusiformis*)

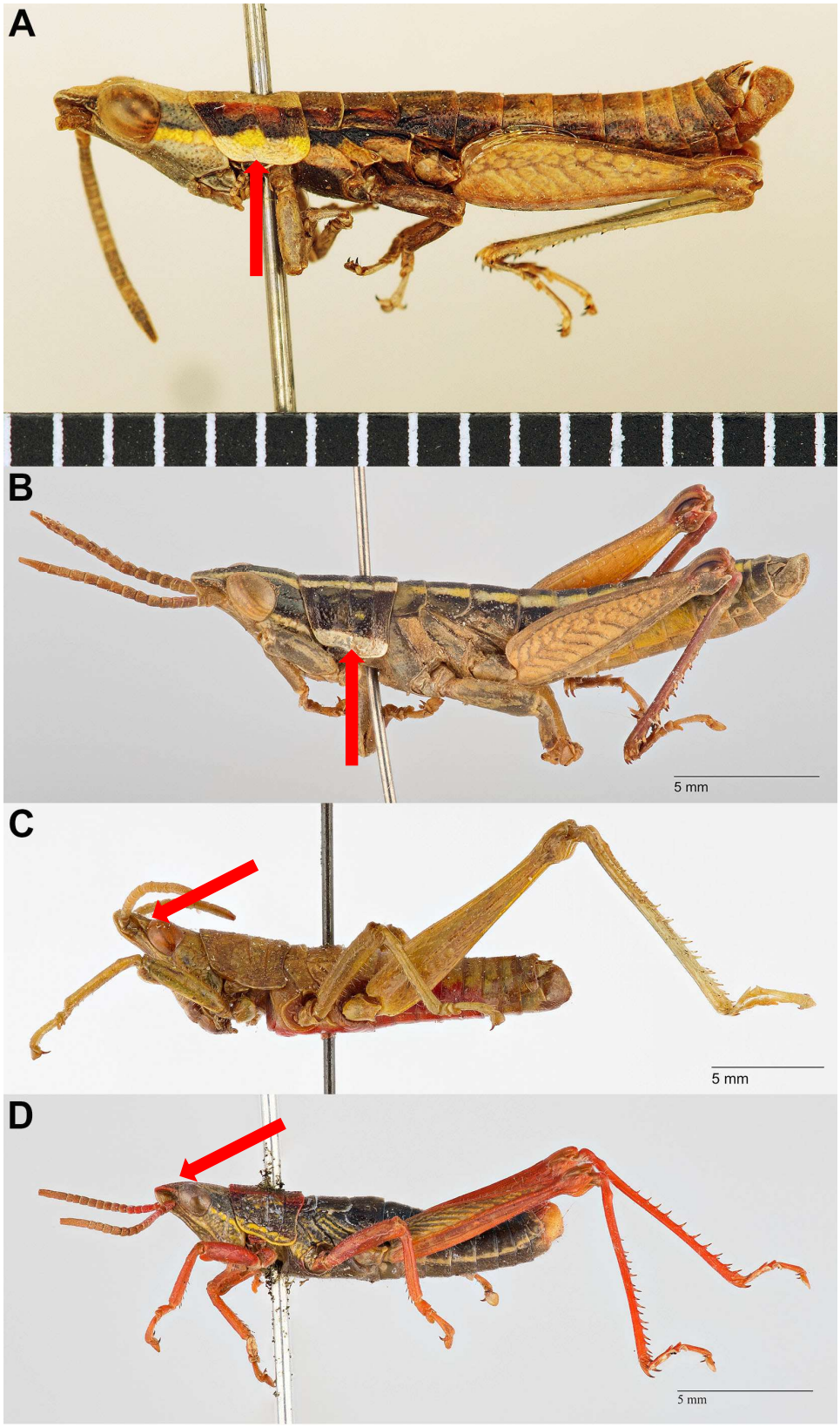

Figure 3.16. African Pyrgomorphidae 7. **A.** *Parorthacris somalica* male lateral view. **B.** *Vittisphena somalica* male lateral view. **C.** *Occidentosphena ruandensis* male lateral view. **D.** *Parasphena imatogensis* male lateral view.

31. Antennae length equal or shorter than head and pronotum together. 34

31’. Antennae length longer than head and pronotum together. 32

32. Posterior part of male subgenital plate wide and flattened; cerci short, wide, compressed angular at apex (fig. 3.17C). (Tanzania, Democratic Republic of the Congo)

.....***Cawendia**** **(1 sp.)**

(*C. glabrata*)

32’. Posterior part of male subgenital plate ridge-like, compressed; cerci long, incurved or straight and downcurved in apical part. 33

33. Male mesosternal interspace as long as or slightly longer than its width; cerci almost straight, in apical half downcurved (fig. 3.17D). (Angola, Zambia, Zimbabwe, Malawi, Mozambique) .....***Pezotagasta**** **(2 spp.)**

(*P. angolensis, P. bredoi*)

33’. Male mesosternal interspace twice as long as its width; cerci strongly incurved (fig. 3.18A). (Central Africa) .....***Humpatella**** **(4 spp.)**

(*H. constricta, H. huambae, H. nigopicta, H. severini*)

34. Posterior margin of pronotum incurved, excised or straight. 35

34’. Posterior margin of pronotum excurved (fig. 3.18B). (South Africa) ……....***Plerisca*** **(2 spp.)**

(*P. peringueyi, P. rubripennulis*)

35. Tegmina reaching the second coxae in lateral view. 36

35’. Tegmina reaching the third coxae in lateral view. 40

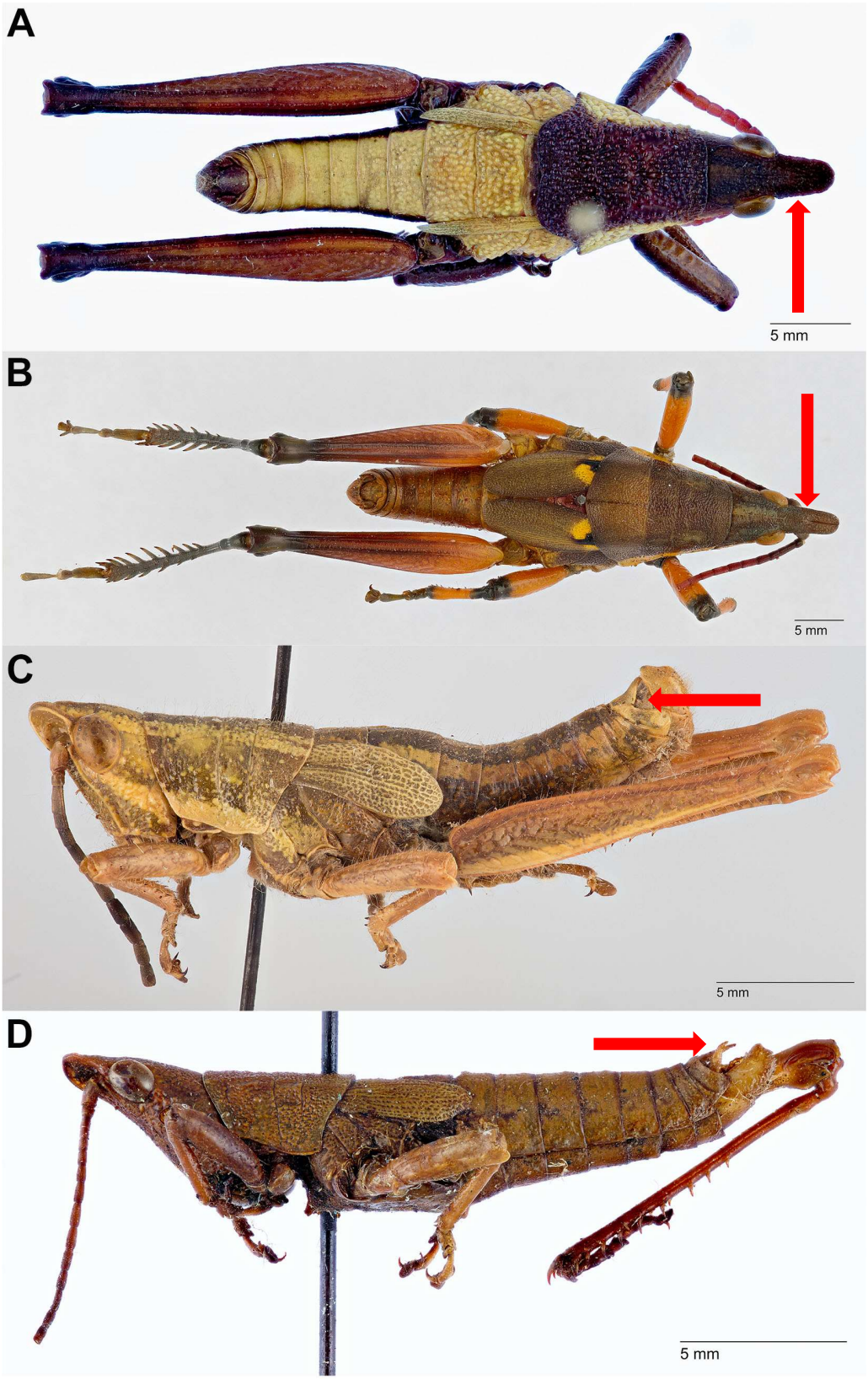

Figure 3.17. African Pyrgomorphidae 8. **A.** *Chirindites odendaali* male dorsal view. **B.** *Sphenexia fusiformis* male dorsal view. **C.** *Cawendia glabrata* male lateral view. **D.** *Pezotagasta angolensis* male lateral view.

36. Tegmina ovoidal. 37

36'. Tegmina elongate. 38

37. Head length equal or almost equal to the length of pronotum (fig. 3.18C). (Somalia) .....***Somalopyrgus**** **(2 spp.)**

(*S. messanai, S. rotundipennis*)

37'. Head length shorter than the length of pronotum (fig. 3.18D). (Kenya). ..***Marsabitacris**** **(1 sp.)**

(*M. citronota*)

38. Integument rugose, tubercles between eyes and pronotum in lateral view. 39

38'. Integument smooth, total body length less than 2 cm. (fig. 3.19A) (Northern Africa) .....***Leptea**** **(2 spp.)**

(*L. albotaeniata, L. debilis*)

39. Cerci triangular; distance between eye and the lateral margin of pronotum equal or larger than the length of eye (fig. 3.19B). (South Africa) .....***Afrosphenella**** **(2 spp.)**

(*A. capensis, A. senecionicola*)

39'. Cerci conical; distance between eye and the lateral margin of pronotum less than the length of eye (fig. 3.19C). (East Africa) .....***Parasphenula*** **(2 spp.)**

(*P. abyssinica, P. boranensis*)

40. Posterior margin of pronotum bilobed (fig. 3.19D). (East and Southern Africa) .....***Parasphenella**** **(4 spp.)**

(*P. carinata, P. dubia, P. forchhammeri, P. meridionalis*)

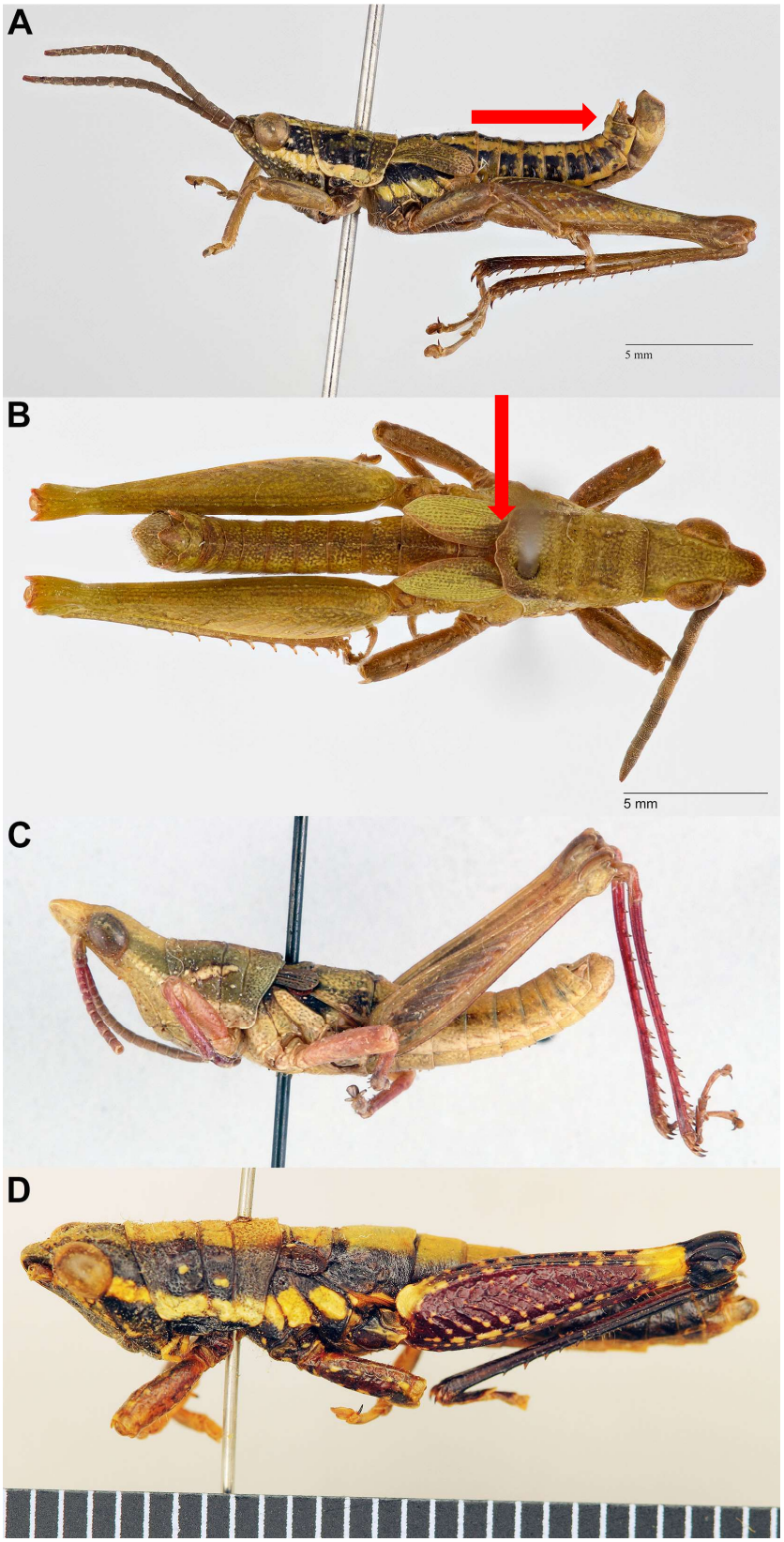

Figure 3.18. African Pyrgomorphidae 9. **A.** *Humpatella huambae* male lateral view. **B.** *Plerisca rubripennulis* male dorsal view. **C.** *Somalopyrgus messanai* male lateral view. **D.** *Marsabitacris citronota* male lateral view.

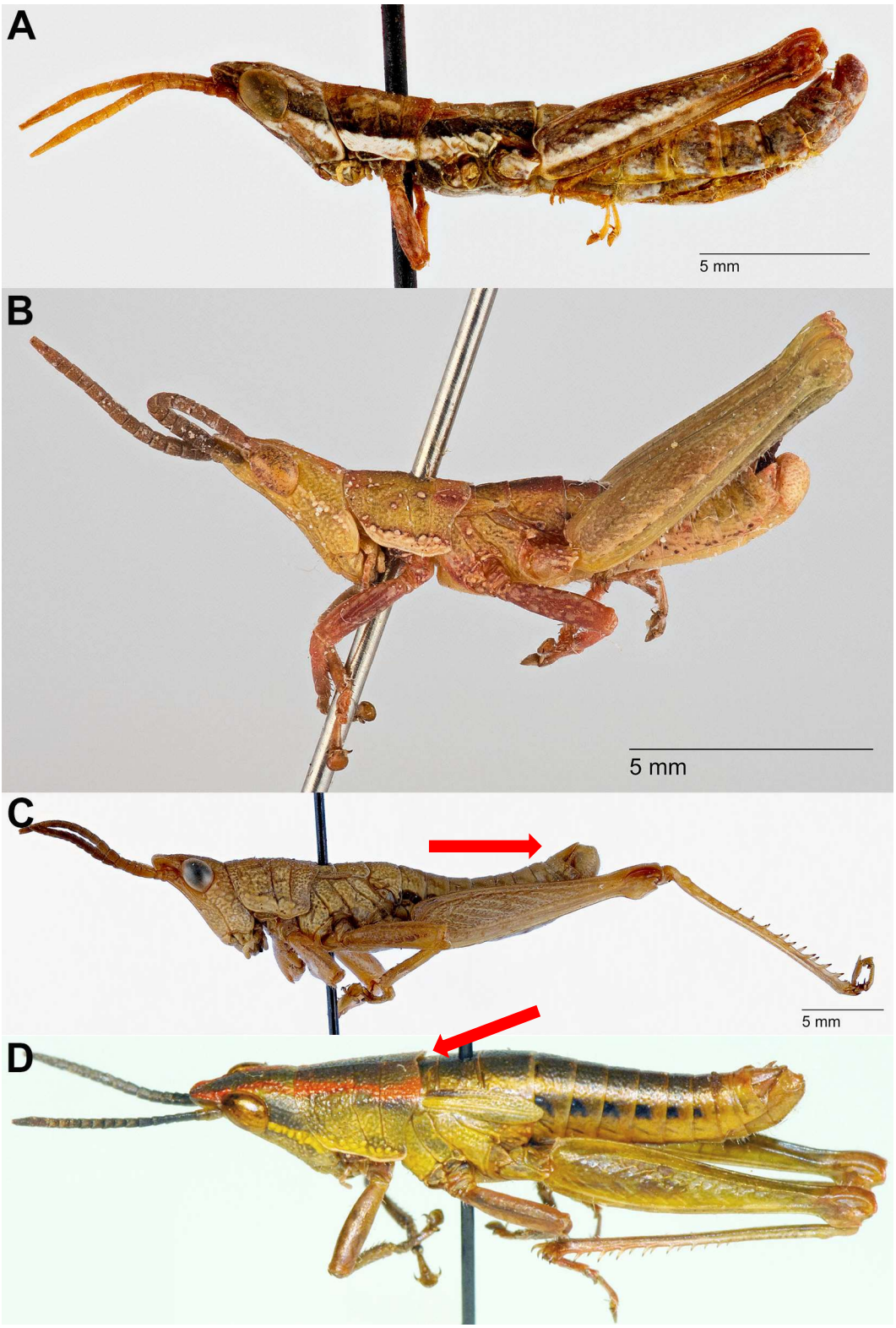

Figure 3.19. African Pyrgomorphidae 10. **A.** *Leptea debilis* male lateral view. **B.** *Afrosphenella capensis* male lateral view. **C.** *Parasphenulla abyssinica* male lateral view. **D.** *Parasphenella carinata* male lateral view.

40’. Posterior margin of pronotum not bilobed. 41

41. Tegmina elongate. 42

41’. Tegmina lobiform (fig. 3.20A). (South Africa) .....***Carinisphena**** **(1 sp.)**

(*C. producta*)

42. Tegmina narrow, with around 5 veins running parallel (fig. 3.20B). (Eastern and Southern Africa) .....***Stenoscepa**** **(11 spp.)**

(*S. fusiformis, S. gallae, S. gracilis, S. grandis, S. granulata, S. maxima, S. montana, S. obscura, S. picta, S. picticeps, S. rhodesiensis*)

42’. Tegmina broad, with around 8 veins running parallel (fig. 3.20C). (Eastern Africa)

.....***Pyrgomorphella*** **(7 spp.)**

(*P. albini, P. arachidis, P. carinulata, P. dicrostachyae, P. minuta, P. sphenarioides, P. tulearensis*)

43. A clear line of tubercles running from behind the eye to the lateral anterior margin of pronotum present. 48

43’. Such a line absent. 44

44. Distance between eye and pronotum in lateral view equal to the length of eye. 45

44’. Distance between eye and pronotum in lateral view twice as long as the length of eye (fig. 3.20D). (Somalia) .....***Xiphipyrgus**** **(1 sp.)**

(*X. tunstalli*)

45. Length of hind femur shorter than or equal to the length of abdomen. 46

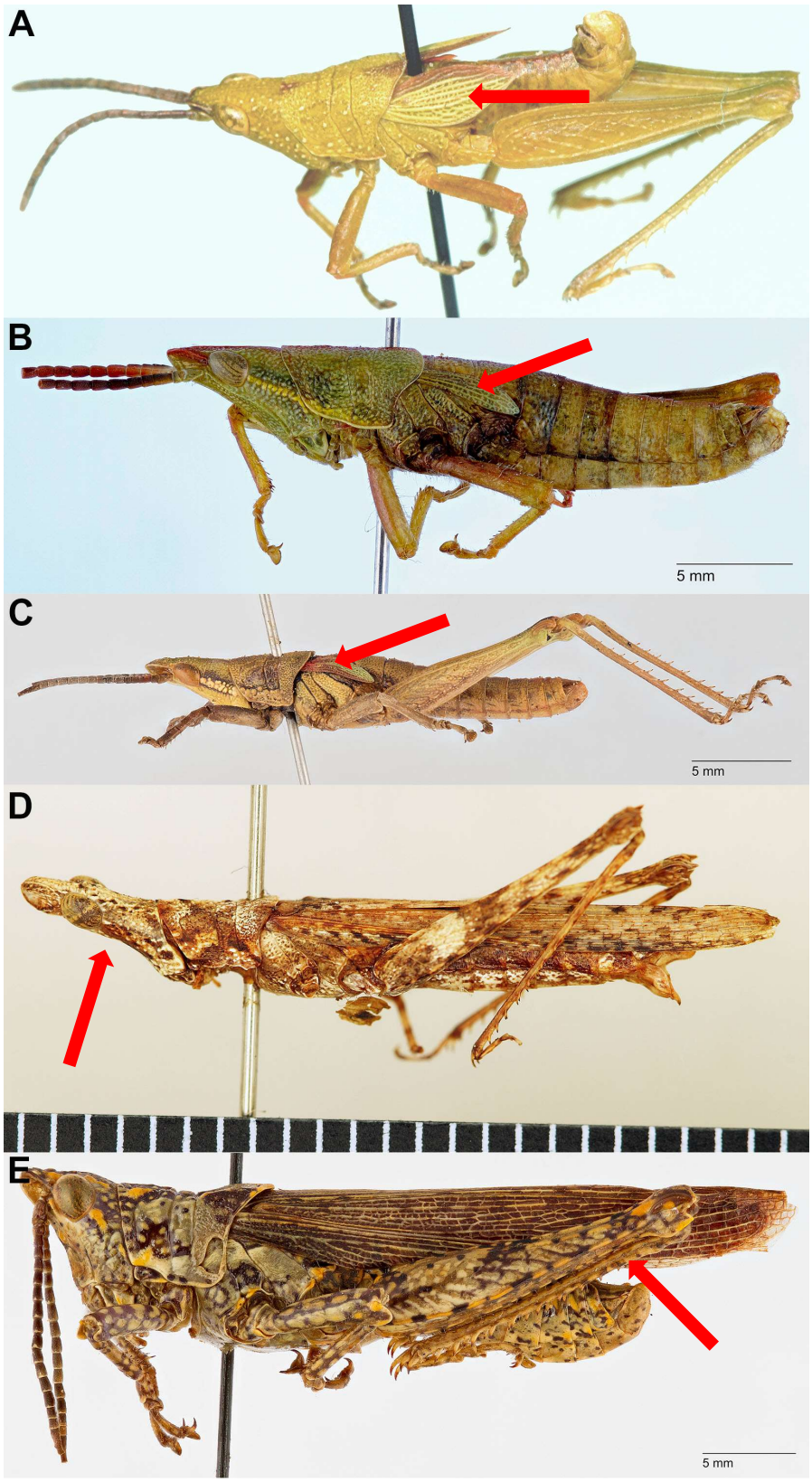

Figure 3.20. African Pyrgomorphidae 11. **A.** *Carinisphena producta* male lateral view. **B.** *Stenoscepa gracilis* male lateral view. **C.** *Pyrgomorphella arachidis* male lateral view. **D.** *Xiphipyrgus tunstalli* female lateral view. **E.** *Ochrophlebia cafra* male lateral view.

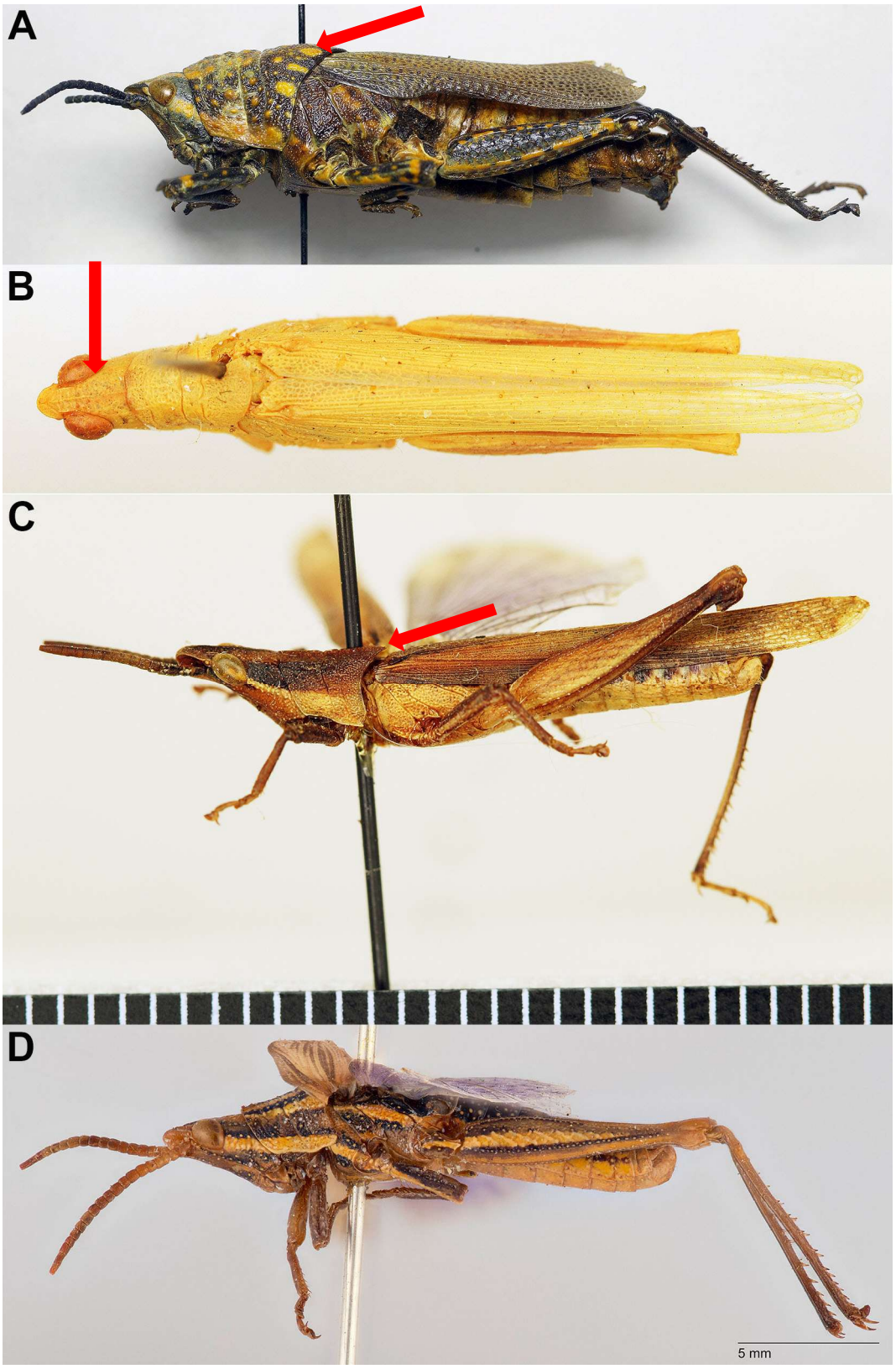

Figure 3.21. African Pyrgomorphidae 12. **A.** *Poekilocerus bufonius* female lateral view. **B.** *Macroleptea laevigata* male dorsal view. **C.** *Eilenbergia sagitta* male lateral view. **D.** *Ochrophlegma violacea* male lateral view.

45’. Length of hind femur longer than the length of abdomen (fig. 3.20E). (Angola and Southern Africa) .....***Ochrophlebia**** **(1 sp.)**

(*O. cafra*)

46. Posterior margin of pronotum not reaching the second coxae. 47

46’. Posterior margin of pronotum reaching the second coxae (fig. 3.21A). (Upper half of Africa) …….....***Poekilocerus*** **(2 spp.)**

(*P. bufonius, P. calotripidis*)

47. A pair of sinuous lines of pustules present in the median area of vertex. (Congo)

.....***Katangacris**** **(1 sp.)**

(*K. enigmatica*)

47’. Such lines absent (fig. 3.21B). (Northern Africa) .....***Macroleptea**** **(1 sp.)**

(*M. laevigata*)

48. Posterior margin of pronotum reaching the second coxae. 49

48’. Posterior margin of pronotum not reaching the second coxae (fig. 3.21C). (Angola)

.....***Eilenbergia**** **(1 sp.)**

(*E. sagitta*)

49. Parallel bands of light and dark colors absent through body. 50

49’. Parallel bands of light and dark colors present on through body (fig. 3.21D). (Southern Africa) .....***Ochrophlegma**** **(3 spp.)**

(*O. pygmaea, O. violacea, O. vittifera*)

50. There are six genera that do not possess consistent characters to distinguish them from each other, even at internal genitalia level. A major revision is required to clearly define these genera. In general, the generic definitions are very vague with several indefinite and conditional characters (Rowell et al. 2013). The taxonomic history of the species in these genera is complex. For instance, the species *Laufferia chloronota* was described as *Ochrophlebia*, The three species of *Protanita* were described as *Tanita*. The species *Scabropyrgus scabrosus* was described as *Ochrophlebia* then transferred to *Tanita* and then back to *Ochrophlebia*. The species *Tanitella prasina* was described as *Ochrophlebia* and *Tanitella sanderi* was described as *Pyrgomorpha* (Cigliano et al., 2018).

Laufferia* **(1 sp.).** Angola (fig. 3.22A).

(*L. chloronota*)

Protanita* **(3 spp.).** Middle third of Africa (fig. 3.22B).

(*P. elongata, P. fusiformis, P. longiceps*)

Pyrgomorpha **(14 spp.).** All Africa (fig. 3.22C).

(*P. angolensis, P. granulata, P. johnseni, P. rugosa, P. vignaudii, P. agarena, P. albotaeniata, P. bispinosa, P. cognata, P. conica, P. lepineyi, P, minuta, P. tricarinata, P vosseleri*)

Scabropyrgus* **(1 sp.).** Angola (fig. 3.22D).

(*S. scabrosus*)

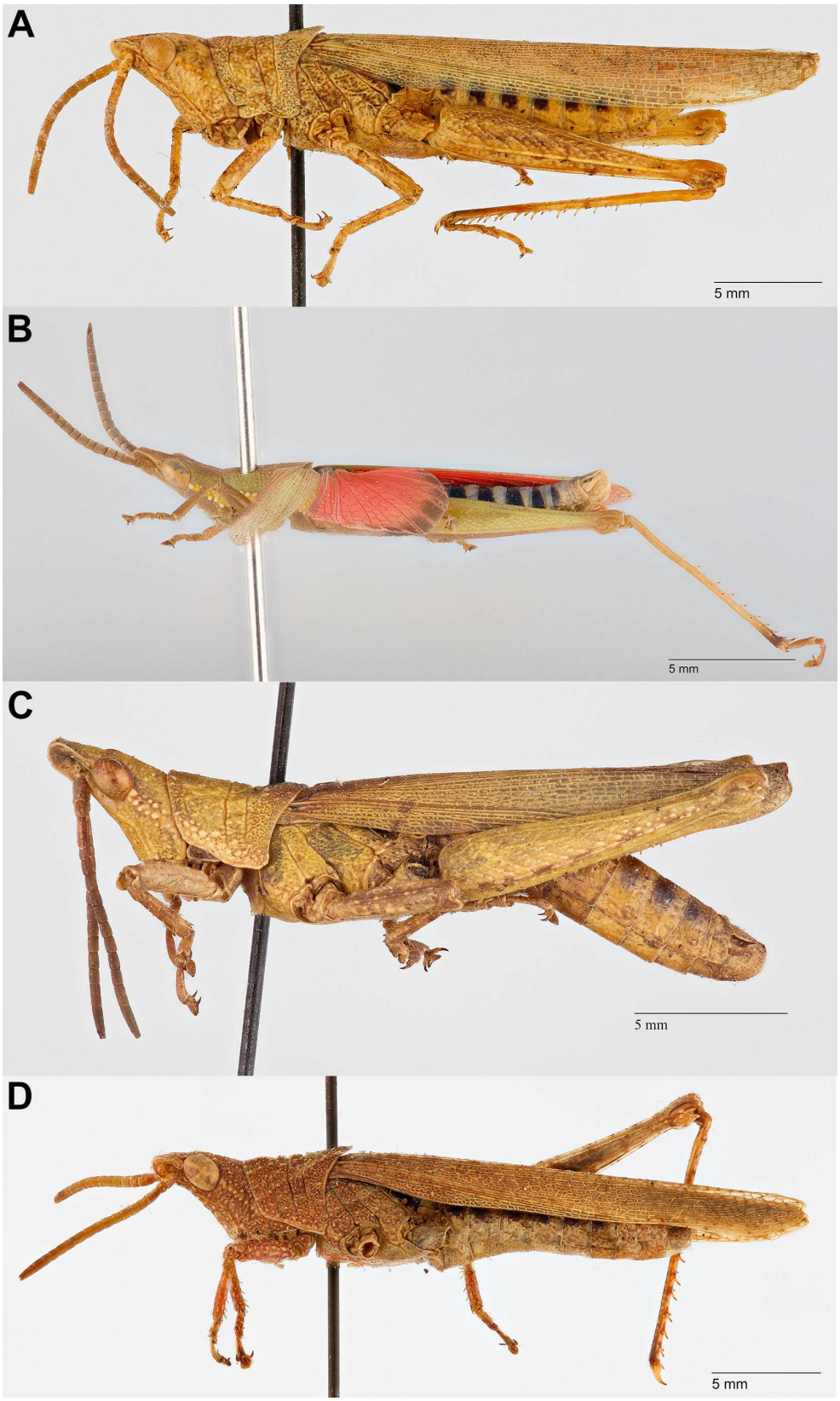

Figure 3.22. African Pyrgomorphidae 13. **A.** *Laufferia chloronota* male lateral view. **B.** *Protanita fusiformis* male lateral view. **C.** *Pyrgomorpha vignaudii* male lateral view. **D.** *Scabropyrgus scabrosus* male lateral view.

***Tanita** (9 spp.).** Sub-Saharan Africa (fig. 3.23A).

(*T. brachyptera, T. breviceps, T. lineaalba, T. loosi, T. parva, T. purpurea, T. rosea, T. stulta, T. subcylindrica*)

***Tanitella** (2 spp.).** Southern Africa (fig. 3.23B).

(*T. prasina, T. sanderi*)

Figure 3.23. African Pyrgomorphidae 14. **A.** *Tanita loosi* male lateral view. **B.** *Tanitella prasina* male lateral view.

3.2.4 Key to Pyrgomorphidae genera of Madagascar

Modified from Dirsh, (1963); Descamps & Wintrebert (1966) and Dirsh & Descamps, (1968).

Twenty genera, sixteen endemic to Madagascar. The genus *Caprorhinus* consists of 27 species, with *C. squamipennis* endemic to Anjouan Island, Comoros.

Zonocerus elegans has been reported for Madagascar as the type locality of the synonym *Z. hova* by Saussure (1899) but no further observation has been recorded and Hollier (2013) registered that the locality "Madagascar" was in the box including the specimen but not it the label of specimen. Based on these reasons I decided to not include in this key. This species is unmistakable in case is collected in Madagascar. *Buyssoniella madecassa* was described by Bolívar in 1905 based on a single female but this specimen is lost and there is no other known specimen (Kevan, 1977), which is why it is also not included in this key.

1. Antennal base present behind the lateral ocelli; marginal area of hind femur not displaced ventrally to the outer medial area; typically with elongated body form, fully winged, with short tegmina or wingless. 2

1'. Antennal base present in front of the lateral ocelli; marginal area of hind femur displaced ventrally to the outer medial area; body form not elongated and fully winged. 17

2. Pronotum strongly tuberculate and toothed, the metazona flattened, lateral lobes forming a right angle with the metazoan (fig. 3.24A,B). .....***Phymateus*** **(2 spp.)**

(*P. madagassus, P. saxosus*)

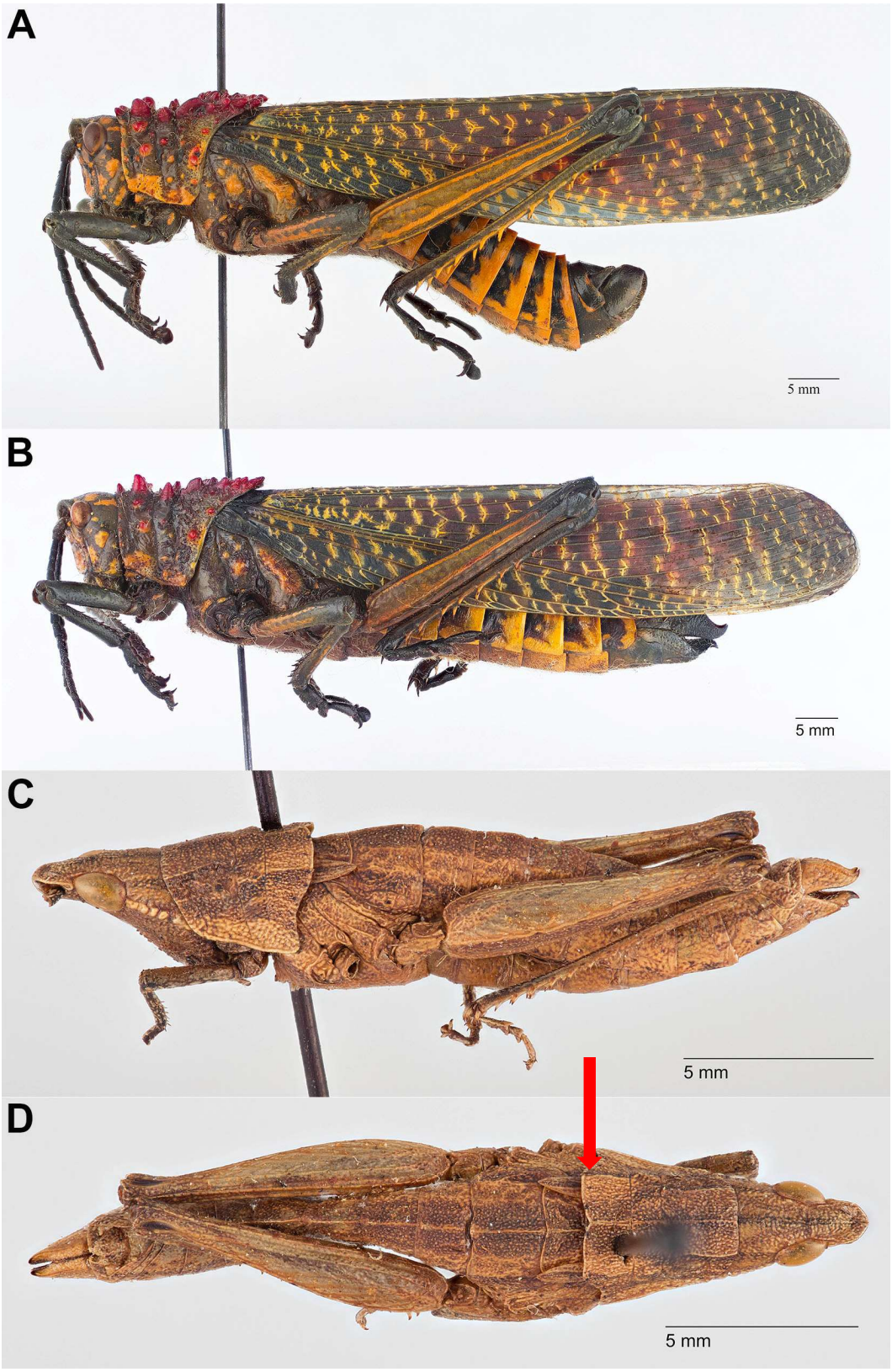

Figure 3.24. Madagascar Pyrgomorphidae 1**. A.** *Phymateus saxosus* male lateral view. **B.** *P. saxosus* female lateral view. **C.** *Pyrgomorphella madecassa* female lateral view. **D.** *P. madecassa* female dorsal view.

2’. Pronotum not tuberculate, or only with small tubercles, and not toothed, cylindrical or sub-cylindrical metazona. 3

3. Tip of head in lateral view without a process formed by the fastigium of vertex and the upper part of forehead; if there is doubt of the presence of such process and the pyrgomorph is wingless, then the male subgenital plate is never protruding. 4

3’ Tip of head in lateral view with a process formed by the fastigium of vertex and the upper part of forehead; male subgenital plate in some cases protruding. 15

4. Tegmina fully developed, reduced or vestigial. 5

4’. Tegmina completely absent. 9

5. Lateral carinae of the pronotum present (fig. 3.24C,D). .....***Pyrgomorphella*** **(4 spp.)**

(*P. dicrostachyae, P. madecassa. P. minuta, P. tulearensis*)

5’. Lateral carinae of the pronotum absent. 6

6. Tegmina reduced and touching dorsally or lobiform and covering the tympanum, sometimes fully developed (in the macropterous form). 7

6’. Vestigial tegmina not covering the tympanum when present. 8

7. Strongly conical head; fastigium of vertex more than twice as long as its width; tegmina lobiform in lateral profile, or fully winged (fig. 3.25A,B). .....***Rubellia****** **(1 sp.)**

(*R. nigrosignata*)

7’. Head less clearly conical; fastigium of vertex just a little longer than its width; brachypterous or macropterous (fig. 3.25C,D). .....***Pseudorubellia****** **(2 spp.)**

(*P. brancsiki, P. thoracica*)

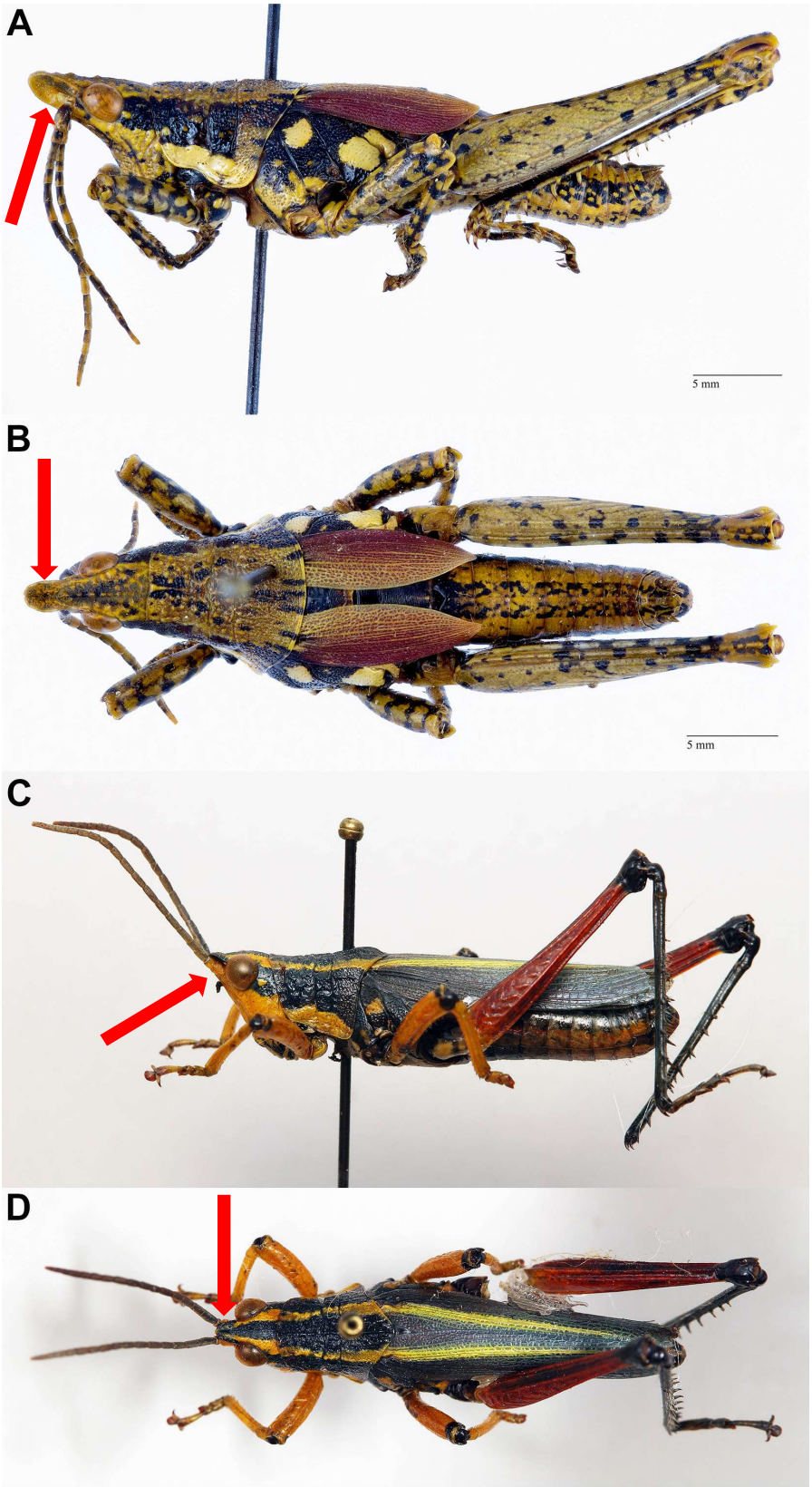

Figure 3.25. Madagascar Pyrgomorphidae 2. **A.** *Rubellia nigrosignata* male lateral view. **B.** *R. nigrosignata* male dorsal view. **C.** *Pseudorubellia thoracica* male lateral view. **D.** *P. thoracica* male dorsal view.

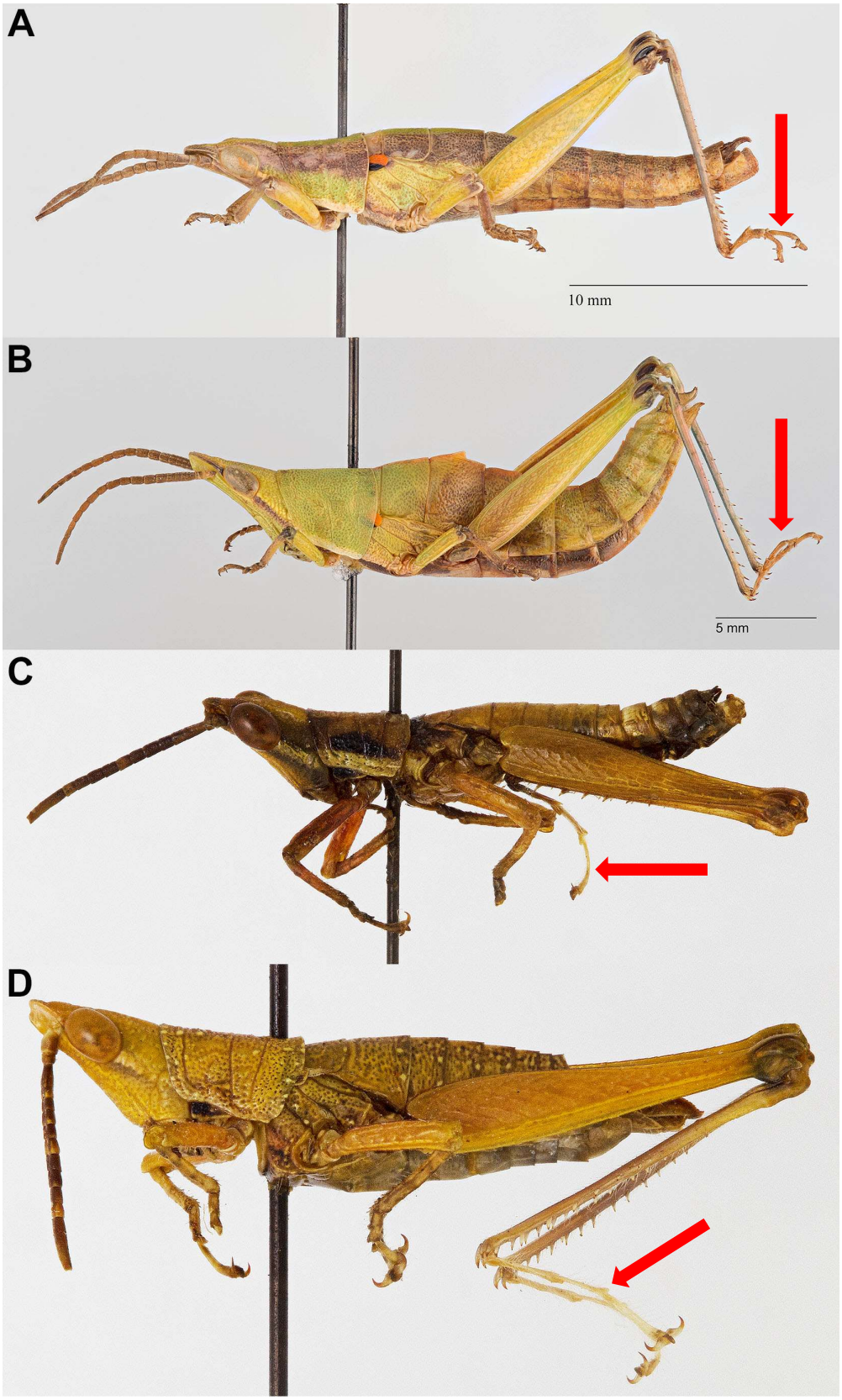

Figure 3.26. Madagascar Pyrgomorphidae 3. **A.** *Caprorhinus kevani* male lateral view. **B.** *C. kevani* female lateral view. **C.** *Malagasphena minor* male lateral view. **D.** *M. minor* female lateral view.

8. Hind tarsi shorter than the half of the hind tibia; arolium larger or equal to the claws; tympanum present (fig. 3.26A,B). .....***Caprorhinus*** **(28 spp.)**

(*C. ambahitae, C. andohahalensis, C. anivoranensis, C. betrokae, C. cadeti, C. dechappei, C. descampsi, C. donskoffi, C. fotadrevensis, C. fusiformis, C. inflatus, C. isoanalae, C. kevani, C. lavanonensis, C. mahabensis, C. major, C. malzyi, C. minor, C. monclari, C. pauliani, C. puerisalbis, C. ralinoroi, C. ranohirae, C. rostratus, C. seyrigi, C. squamipennis* (Comoros)*, C. tenikae, C. zolotarevskyi*)

8'. Hind tarsi almost half the length of the hind tibia; arolium smaller than the claws; tympanum absent (fig. 3.26C,D). .....***Malagasphena*** **(1 sp.)**

(*M. minor*)

9. Tip of head in profile, not indented before touching with the fastigium of vertex. ……....10

9'. Tip of head in profile, notched before touching with the fastigium of vertex. 14

10. Short head, conical or subconical; fastigium of vertex wider than its length; male cerci laterally compressed at the base. 11

10'. Elongated head, conical; fastigium of vertex longer than its width; male cerci simple, conical or subconical. 12

11. Male cerci exceeding the end of the subgenital plate, with the posterior half strongly thinning; posterior margin of pronotum in female straight (fig. 3.27A,B). .....***Gymnohippus*** **(1 sp.)**

(*G. marmoratus*)

11'. Male cerci not longer than its width at the base, triangular in profile; posterior margin of female pronotum at acute angle (fig. 3.27C,D). .....***Acropyrgus*** **(1 sp.)**

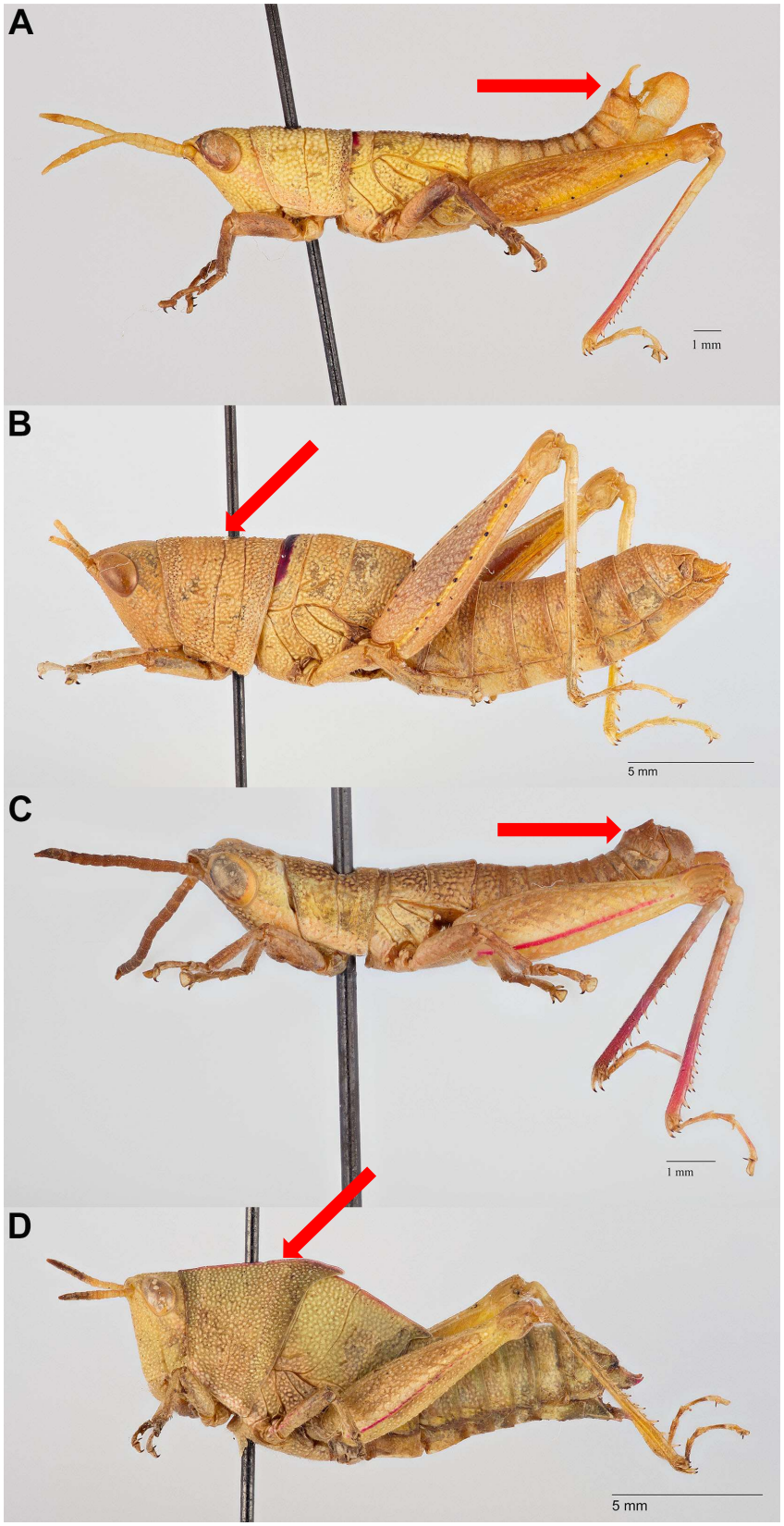

Figure 3.27. Madagascar Pyrgomorphidae 4. **A.** *Gymnohippus marmoratus* male lateral view. **B.** *G. marmoratus* female lateral view. **C.** *Acropyrgus cadeti* male lateral view. **D.** *A. cadeti* female lateral view.

(*A. cadeti*)

12. Male subgenital plate simple, slightly compressed, with rounded apex in lateral view. 13

12'. Male subgenital plate trilobate in dorsal view, the lobes formed by 2 lateral carinae and 1 medial carinula (fig. 3.28A,B). .....***Ambositracris**** **(3 spp.)**

(*A. morati, A. ornata, A.vittata*)

13. Elongated and subcylindrical body in the male, slightly fusiform in the female; sides of the mesosternal space slightly curved or straight; abdomen smooth (fig. 3.28C,D).

.....***Pseudosphena**** **(1 sp.)**

(*P. dispar*)

13'. Cylindrical body and very elongated in both sexes; sides of the mesosternal space strongly curved; abdomen tuberculate (fig. 3.28E,F). .....***Dyscolorhinus**** **(2 spp.)**

(*D. squalinus, D. vittatus*)

14. Very thin, elongated, cylindrical body; fastigium of the vertex strongly elongated, angular, more than twice as long as wide; antennae longer than head and pronotum combined (fig. 3.29A,B). .....***Sagittacris**** **(1 sp.)**

(*S. malagassa*)

14'. Cylindrical or slightly fusiform body; fastigium of vertex parabolic, shorter or less than 2 times longer than its width; antennae shorter than head and pronotum combined (fig. 3.29C,D). .....***Pyrgohippus**** **(2 spp.)**

(*P. pallidus*, *P. productus*)

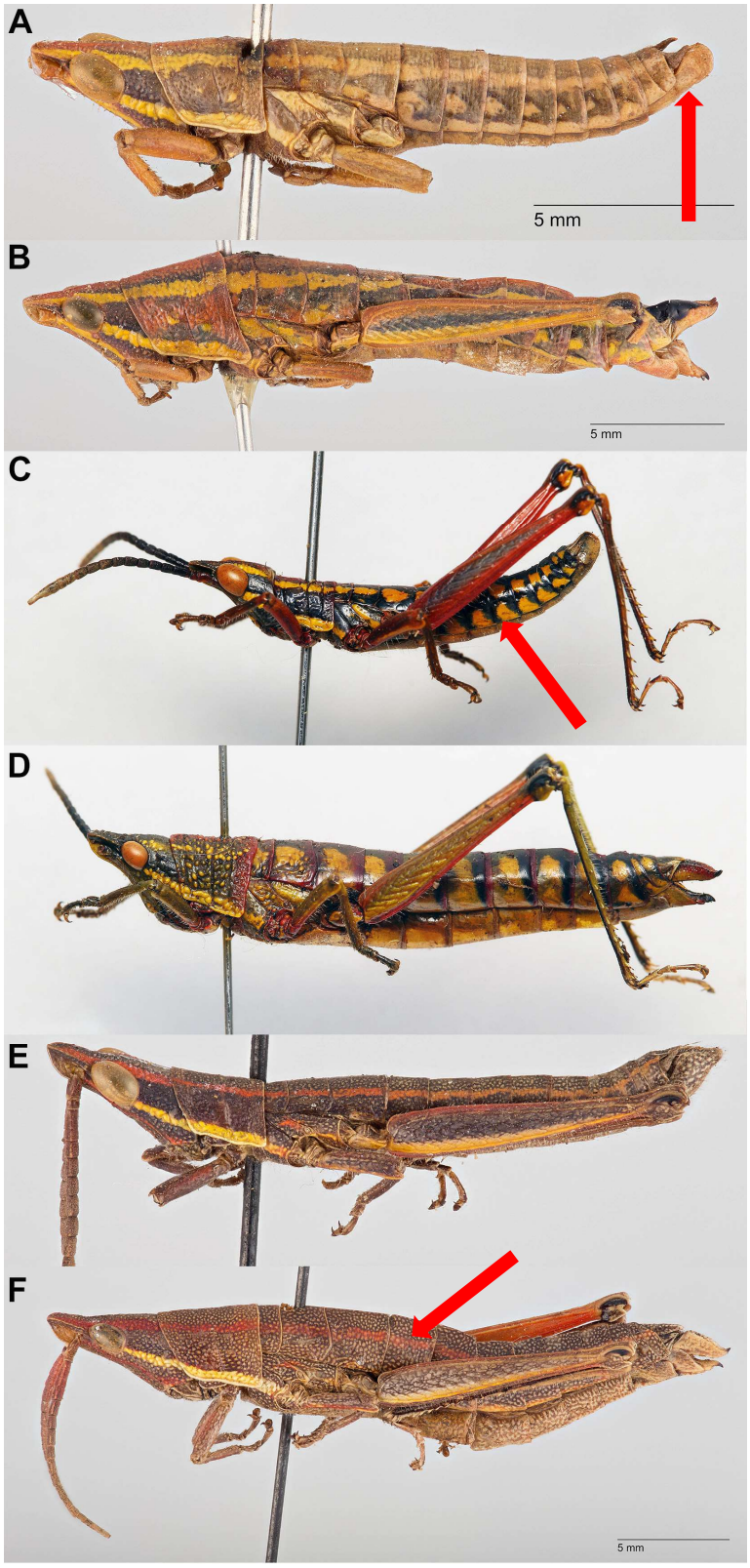

Figure 3.28. Madagascar Pyrgomorphidae 5. **A.** *Ambositacris vittata* male lateral view. **B.** *A. vittata* female lateral view. **C.** *Pseudosphena dispar* male lateral view. **D.** *P. dispar* female lateral view. **E.** *Dyscolorhinus squalinus* male lateral view. **F.** *D. squalinus* female lateral view.

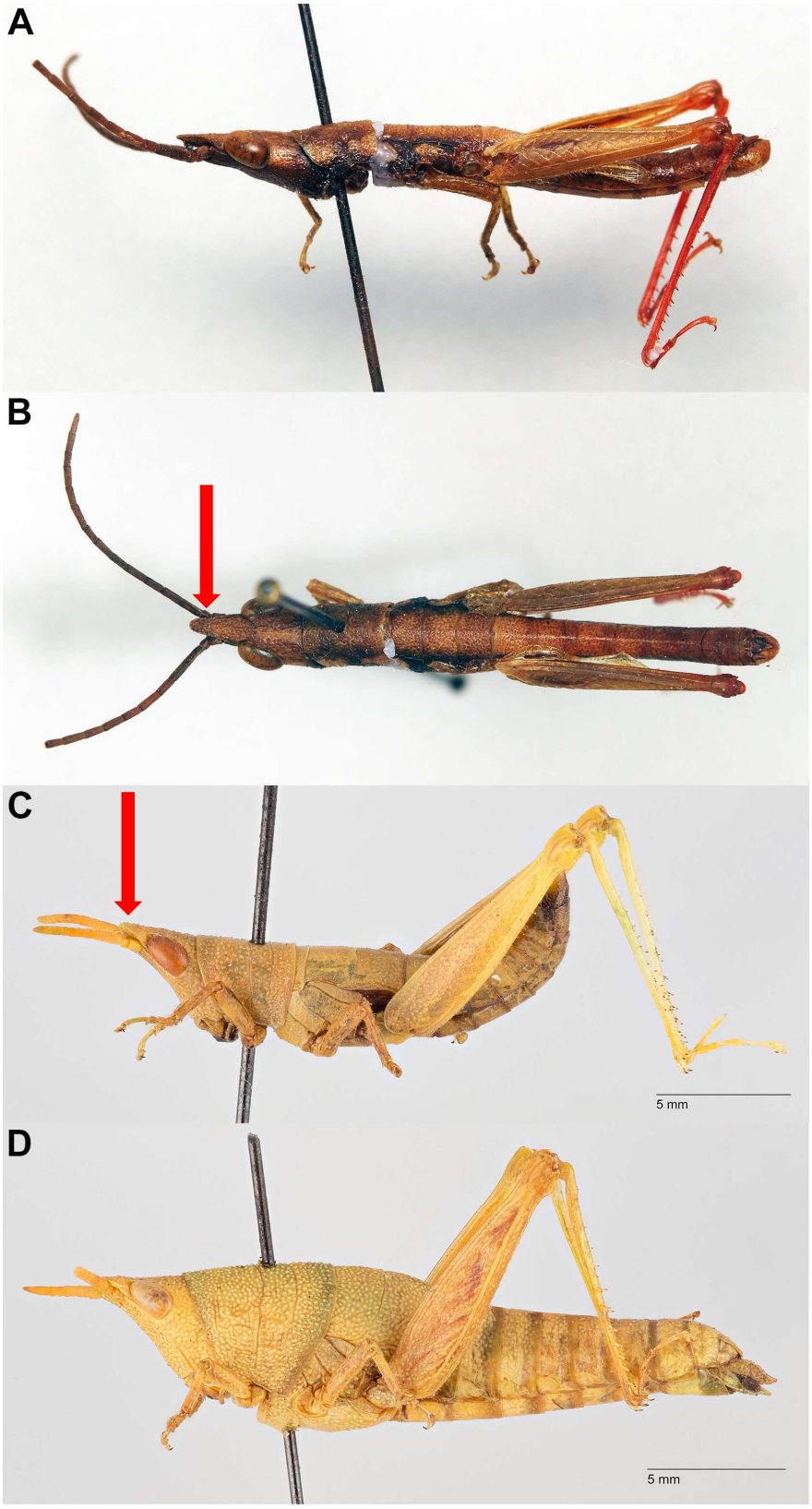

Figure 3.29. Madagascar Pyrgomorphidae 6. **A.** *Sagittacris malagassa* male lateral view. **B.** *S. malagassa* male dorsal view. **C.** *Pyrgohippus pallidus* male lateral view. **D.** *P. pallidus* female lateral view.

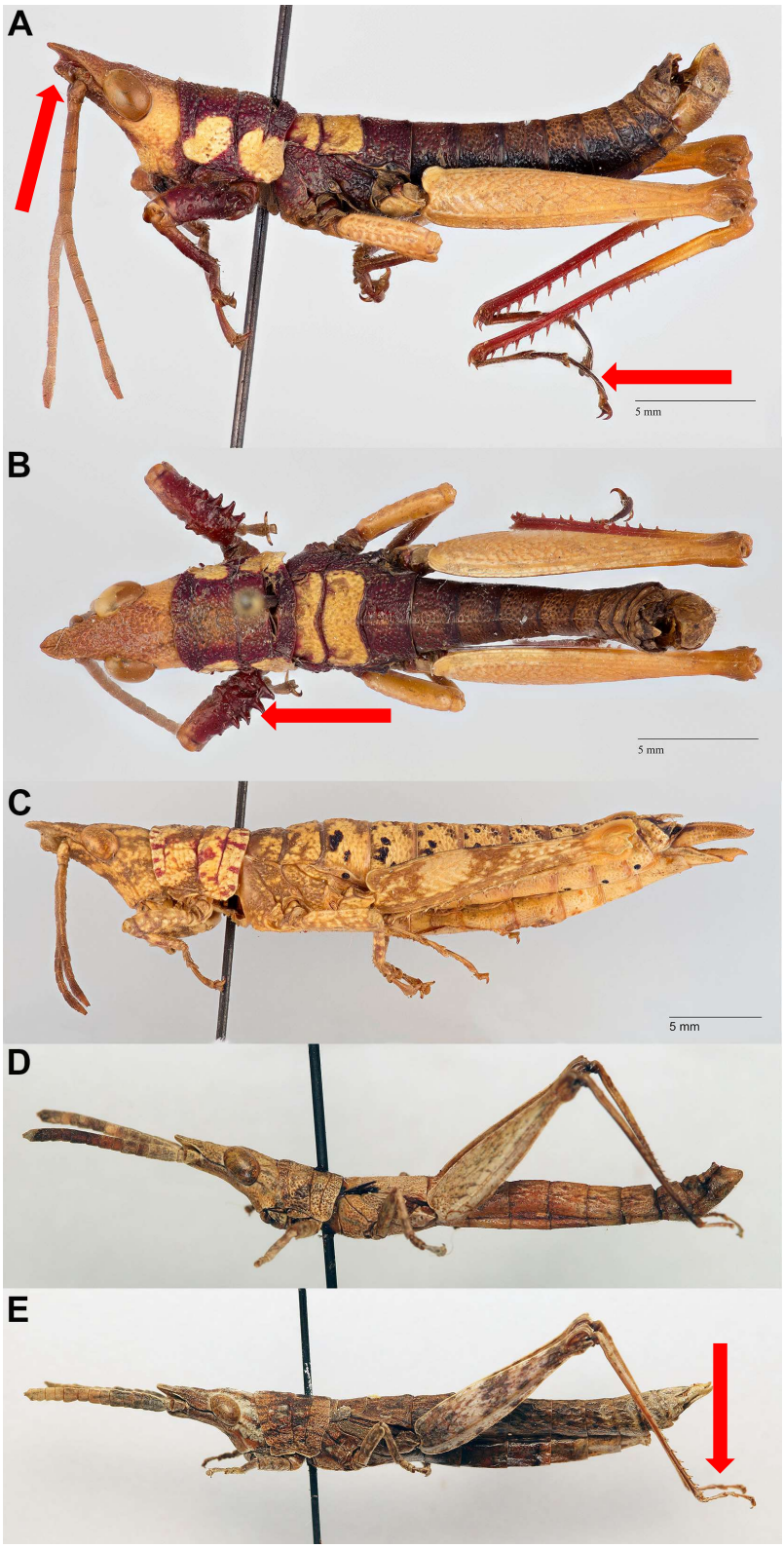

Figure 3.30. Madagascar Pyrgomorphidae 7. **A.** *Acanthopyrgus finoti* male lateral view. **B.** *A. finoti* male dorsal view. **C.** *A. finoti* female lateral view. **D.** *Geloius tanalensis* male lateral view. **E.** *G. tanalensis* female lateral view.

15. Hind tarsi at least equal to the half the length of the hind tibia; anterior femur of male widened and armed with a row of strong spines on the outer side; vestigial tegmina (fig. 3.30A,B,C). .....***Acanthopyrgus** (2 spp.)**

(*A. finoti, A. longicornis*)

15‘. Posterior tarsi shorter than half of the corresponding tibia; anterior femur of males not widened and unarmed. 16

16. Subgenital plate of male not protuding; micropterous (fig. 3.30D,E). .....***Geloius** (3 spp.)**

(*G. crassicornis, G. nasutus, G. tanalanensis*)

16’. Subgenital plate of males strongly dilated; wingless or micropterous (fig. 3.31A,B). .....***Pseudogeloius** (5 spp.)**

(*P. affinis, P. decorsei, P. fotadrevae, P. marolintae, P. relictus*)

17. Macropterous; tip of head in lateral view, not projecting or notched at the apex. ...18

17’. Micropterous or wingless; tip of head in lateral view compressed and protruding towards the middle, notched in profile, at the apex (fig. 3.31C,D). .....***Uhagonia** (3 spp.)**

(*U. depressa, U. sphenarioides, U. wintreberti*)

18. Marginal area of the posterior femur strongly enlarged and displaced ventrally towards the medial area (fig. 3.32C,D). .....***Schulthessia** (1 sp.)**

(*S. biplagiata*)

18’. Marginal area of the posterior femur narrow, displaced little towards the external medial area (fig. 3.32A,B). .....***Atractomorpha* (1 sp.)**

(*A. acutipennis*)

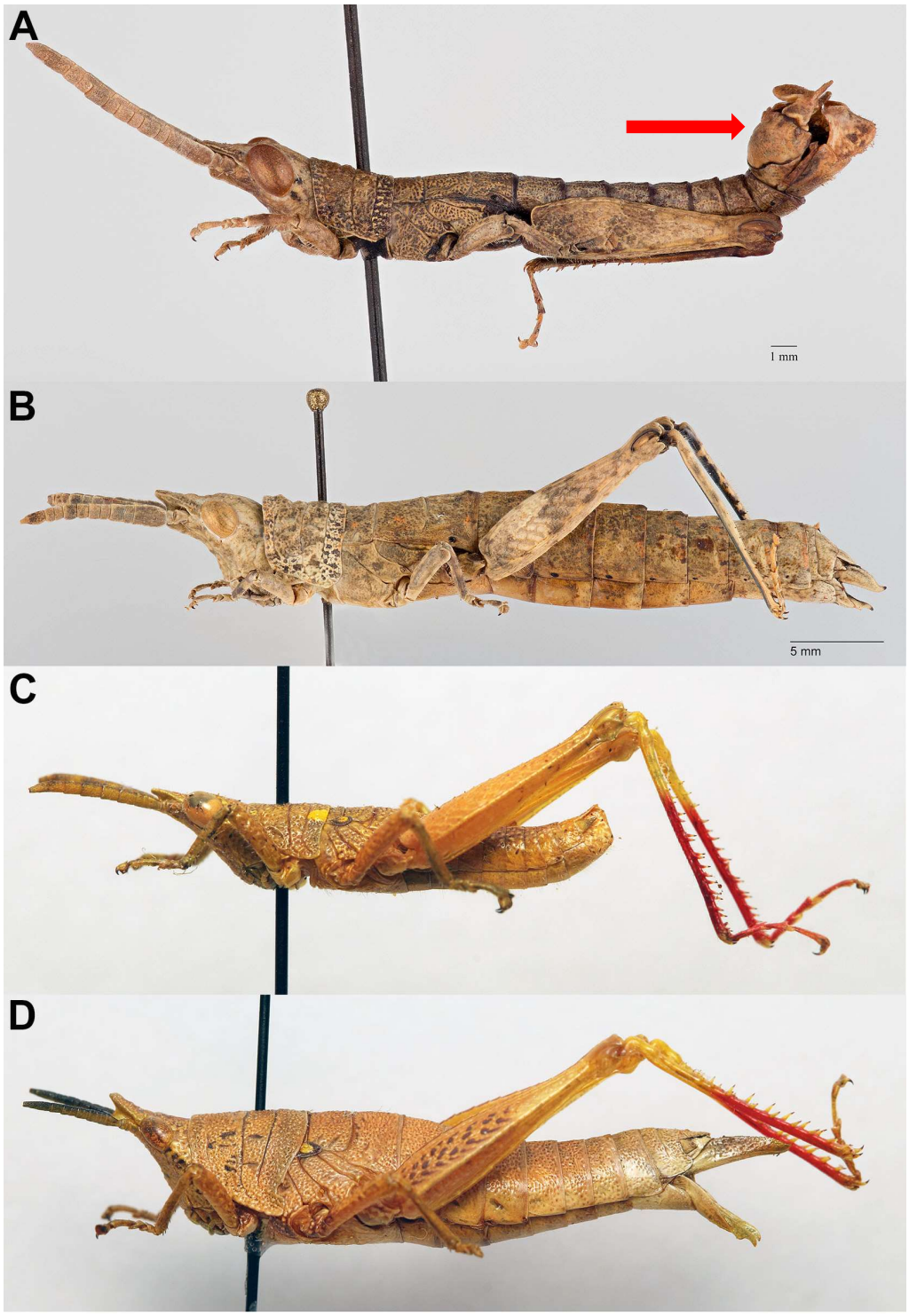

Figure 3.31. Madagascar Pyrgomorphidae 8. **A.** *Pseudogeloius decorsei* male lateral view. **B.** *P. decorsei* female lateral view. **C.** *Uhagonia wintreberti* male lateral view. **D.** *U. wintreberti* female lateral view.

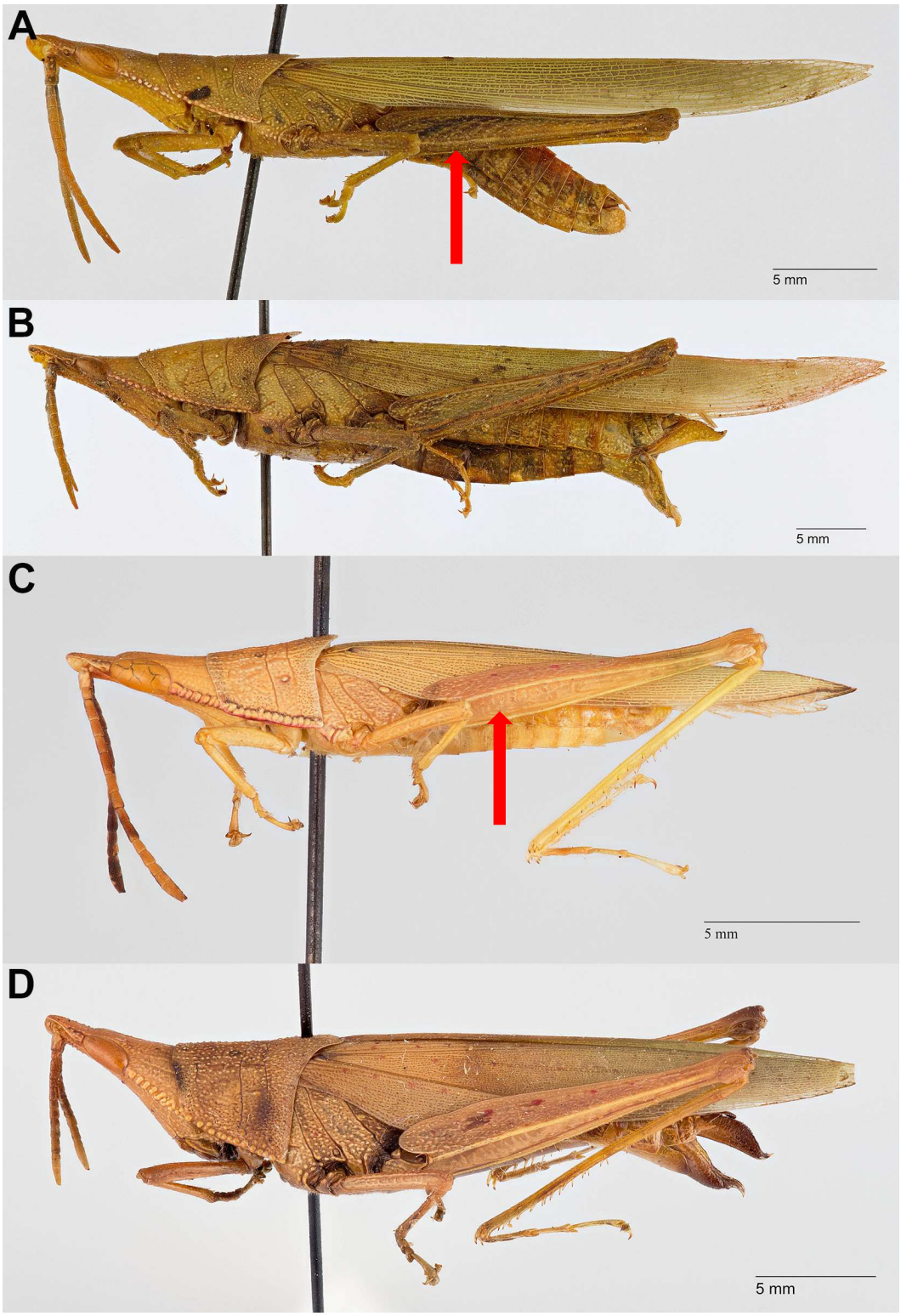

Figure 3.32. Madagascar Pyrgomorphidae 9. **A.** *Atractomorpha acutipennis* male lateral view. **B.** *A. acutipennis* female lateral view. **C.** *Schulthessia biplagiata* male lateral view. **D.** *S. biplagiata* female lateral view.

3.2.5 Key to Pyrgomorphidae genera of China

Modified from Xia Kailing et al. (1994) with information from Huang (1990).

Eleven genera, three endemic.

1. Tegmina well developed. 2

1'. Tegmina absent or highly reduced. 9

2. Head in lateral view forming almost a right angle; pronotum with tubercles or spines.

.....3

2'. Head in lateral view forming an acute angle; pronotum lacking tubercles or spines.

.....4

3. Prozona with a large bilobed tubercle; tegmina frequently with spots; cells numerous with some pentagonal cells towards the posterior end (fig. 3.33A). (Southern China)

.....***Aularches*** **(1 sp.)**

(*A. miliaris*)

3'. Prozona with spines; tegmina without spots; cells less numerous and rectangular (fig. 3.3B). (Southern China) .....***Phymateus*** **(1 sp.)**

(*P. viridipes*)

4. Anterior margin of prosternum forming a wide collar, covering the posterior and lower part of the mouth (fig. 3.2E & 3.33C). (Northwest, Central and Northeast China)

.....***Chrotogonus*** **(2 spp.)**

(*C. armatus, C. turanicus*)

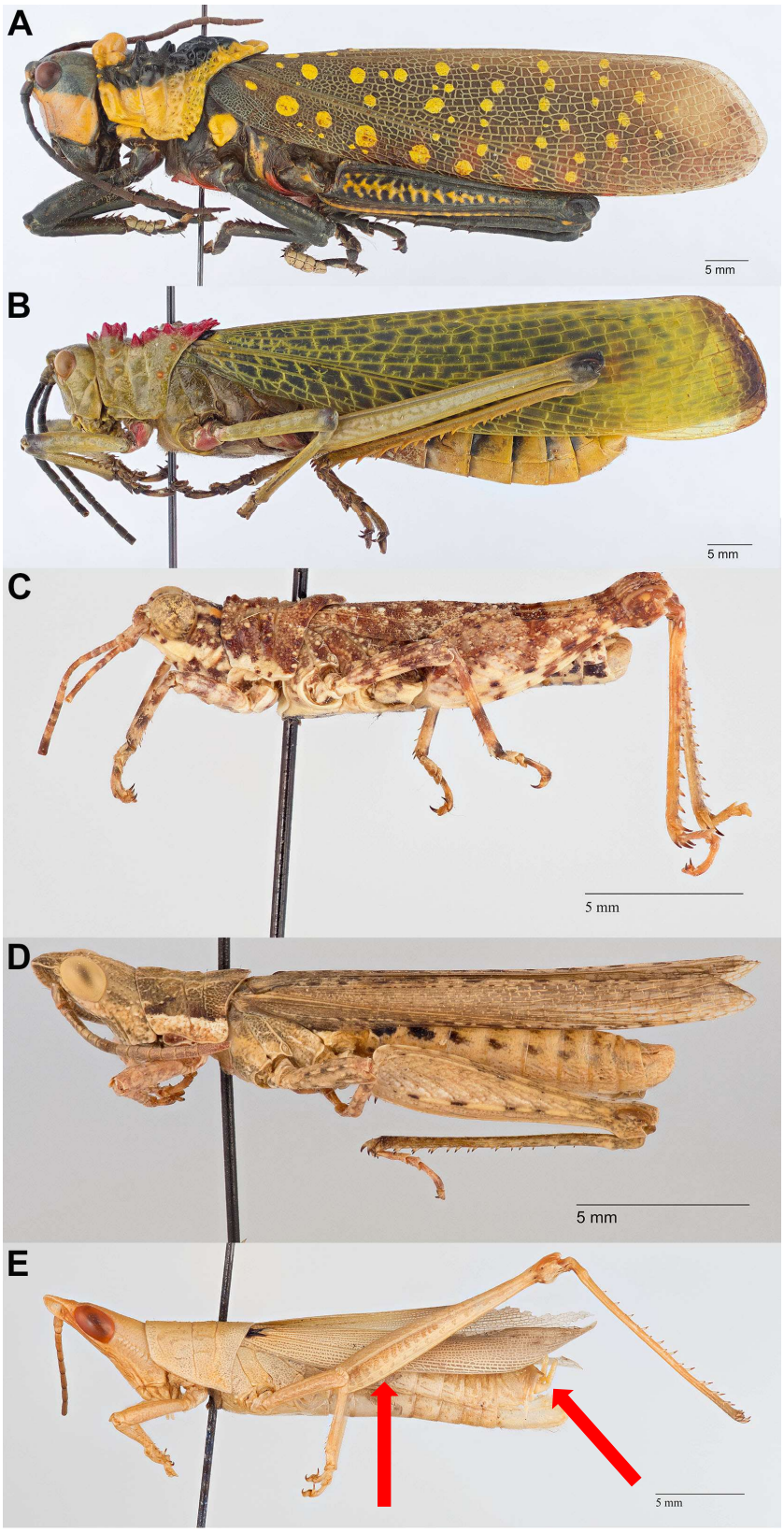

Figure 3.33. China Pyrgomorphidae 1. **A.** *Aularches miliaris* male lateral view. **B.** *Phymateus viridipes* male lateral view. **C.** *Chrotogonus oxypterus* male lateral view. **D.** *Pyrgomorpha conica* male lateral view. **E.** *Pseudomorphacris notata* male lateral view.

4’. Anterior margin of prosternum not covering the posterior and lower part of the mouth.

.....5

5. The base of the antennae present in front of the lateral ocelli. 7

5’. The base of the antennae present below the lateral ocelli. 6

6. Tegmina fully developed; lateral carinae of pronotum well marked (fig. 3.33D).

(Northwestern China) .....***Pyrgomorpha*** **(2 spp.)**

(*P. bispinosa, P. conica*)

6’. Tegmina shortened; lateral carinae of pronotum faintly present (fig. 3.41D). (Yunnan)

.....***Chlorizeina*** **(1 sp.)**

(*C. yunnana*)

7. Marginal area of hind femur expanded, as wide as medial area; cerci bent (fig. 3.33E).

(Southern China) .....***Pseudomorphacris*** **(1 sp.)**

(*P. hollisi*)

7’. Marginal area of hind femur not expanded, narrower than medial area; cerci straight.

.....8

8. The line of tubercles behind eyes not continuing to the lateral margin of pronotum (fig.

3.34A). (Southern China) .....***Tagasta*** **(6 spp.)**

(*T. brachyptera, T. indica, T. nigritibia, T. rufomaculata, T. tonkinensis, T. yunnana*)

8’. The line of tubercles behind eyes continuing to the lateral margin of pronotum (fig.

3.34B). (East half of China, Himalaya) .....***Atractomorpha*** **(15 spp.)**

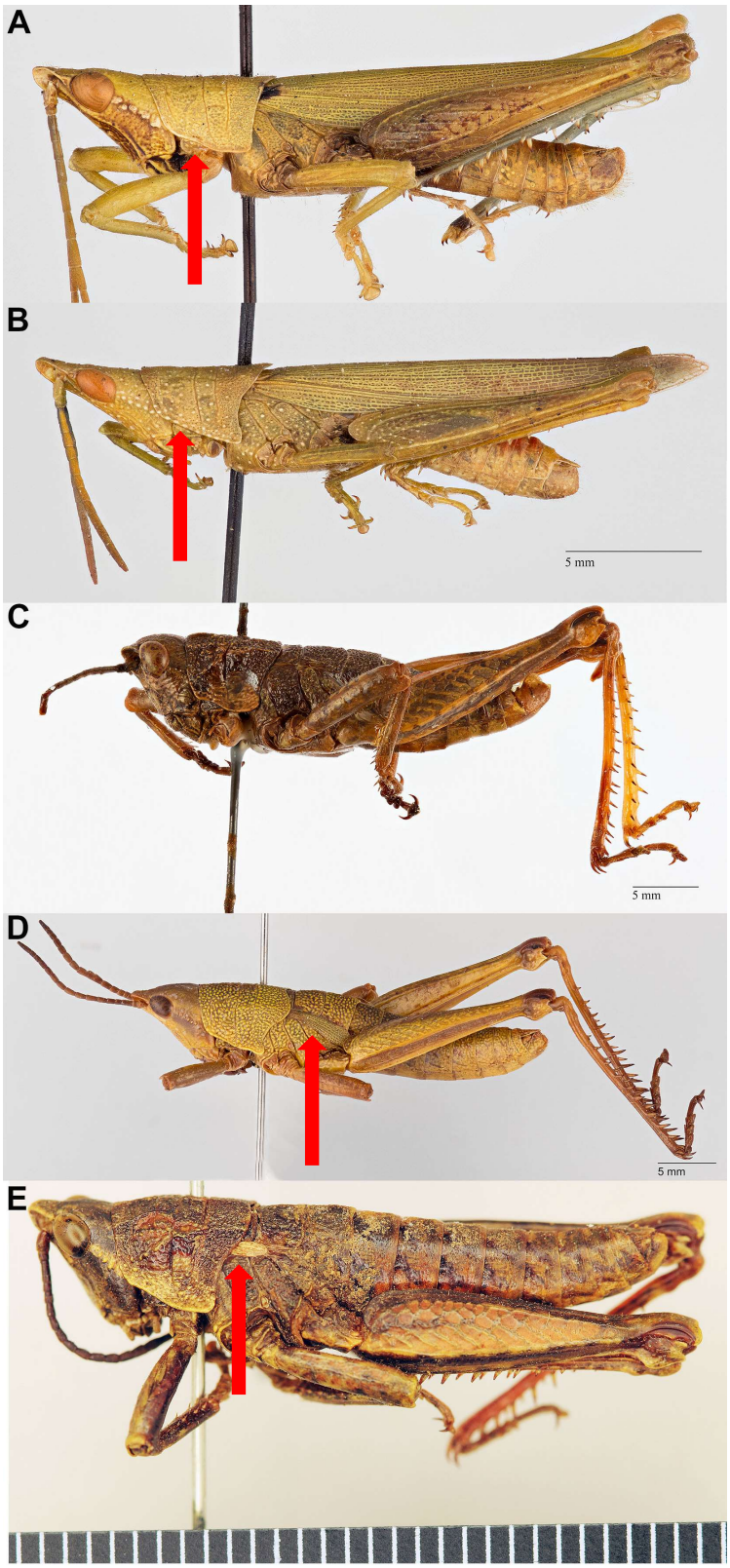

Figure 3.34. China Pyrgomorphidae 2. **A.** *Tagasta indica* male lateral view. **B.** *Atractomorpha aberrans* male lateral view. **C.** *Mekongiella kingdoni* male lateral view. **D.** *Yunnanites coriacea* male lateral view. **E.** *Mekongiana gregoryi* male lateral view.

(*A. burri, A. fuscipennis, A. heteroptera, A. himalayica, A. lata, A. melanostriga, A. micropenna, A. nigripennis, A. peregrina, A. psittacina, A. sagittaris, A. sinensis, A. suzhouensis, A. yunnanensis*)

9. Tympanum present or atrophied. 10

9'. Tympanum absent (fig. 3.34C). (Tibet) .....***Mekongiella* (5 spp.)**

(*M. kingdoni, M. pleurodilata, M. rufitibia, M. wardi, M. xizangensis*)

10. Tegmina present. 11

10'. Tegmina absent. (Yunnan) …….***Paramekongiella** (1 sp.)**

(*P. zhongdianensis*)

11. Tegmina elongated; body with small tubercles; tympanum well developed (fig. 3.34D). (Yunnan) .....***Yunnanites** (3 spp.)**

(*Y. albomarginata, Y. coriacea, Y. zhengi*)

11'. Tegmina reduced; body rugose; tympanum membrane highly reduced, almost closed (fig. 3.34E). (Yunnan) .....***Mekongiana** (2 spp.)**

(*M. gregoryi, M. xiangchengensis*)

3.2.6 Key to Pyrgomorphidae genera of Western Asia

Following Orthoptera Species File (Cigliano et al., 2018) this area corresponds to Afghanistan, Cyprus, Iran, Iraq, Lebanon, Syria, Palestine, Israel, Jordan and Turkey.

Four genera, none endemic to the area.

1. Anterior margin of prosternum covering the posterior and lower part of the mouth (fig. 3.2E). 2

1'. Anterior margin of prosternum not covering the posterior and lower part of the mouth. 3

2. Spurs of hind tibia longer than the basal tarsal segment; middle femur thin and strongly elongated, as long as or longer than head and pronotum together; lower basal lobe of hind femur shorter than the upper one (fig. 3.35A). .....***Tenuitarsus*** **(1 sp.)**

(*T. angustus*)

2'. Spurs of hind tibia shorter than the basal tarsal segment; middle femur short, much shorter than head and pronotum together; lower basal lobe of hind femur longer than the upper one (fig. 3.35B). .....***Chrotogonus*** **(1 sp.)**

(*C. trachypterus*)

3. Antennae base present below lateral ocelli (fig. 3.35C). .....***Pyrgomorpha*** **(6 spp.)**

(*P. bispinosa, P. cognata, P. conica, P. cypria, P. granosa, P. guentheri*)

3'. Antennae base present in front of lateral ocelli (fig. 3.35D). .....***Atractomorpha*** **(1 sp.)**

(*A. acutipennis*)

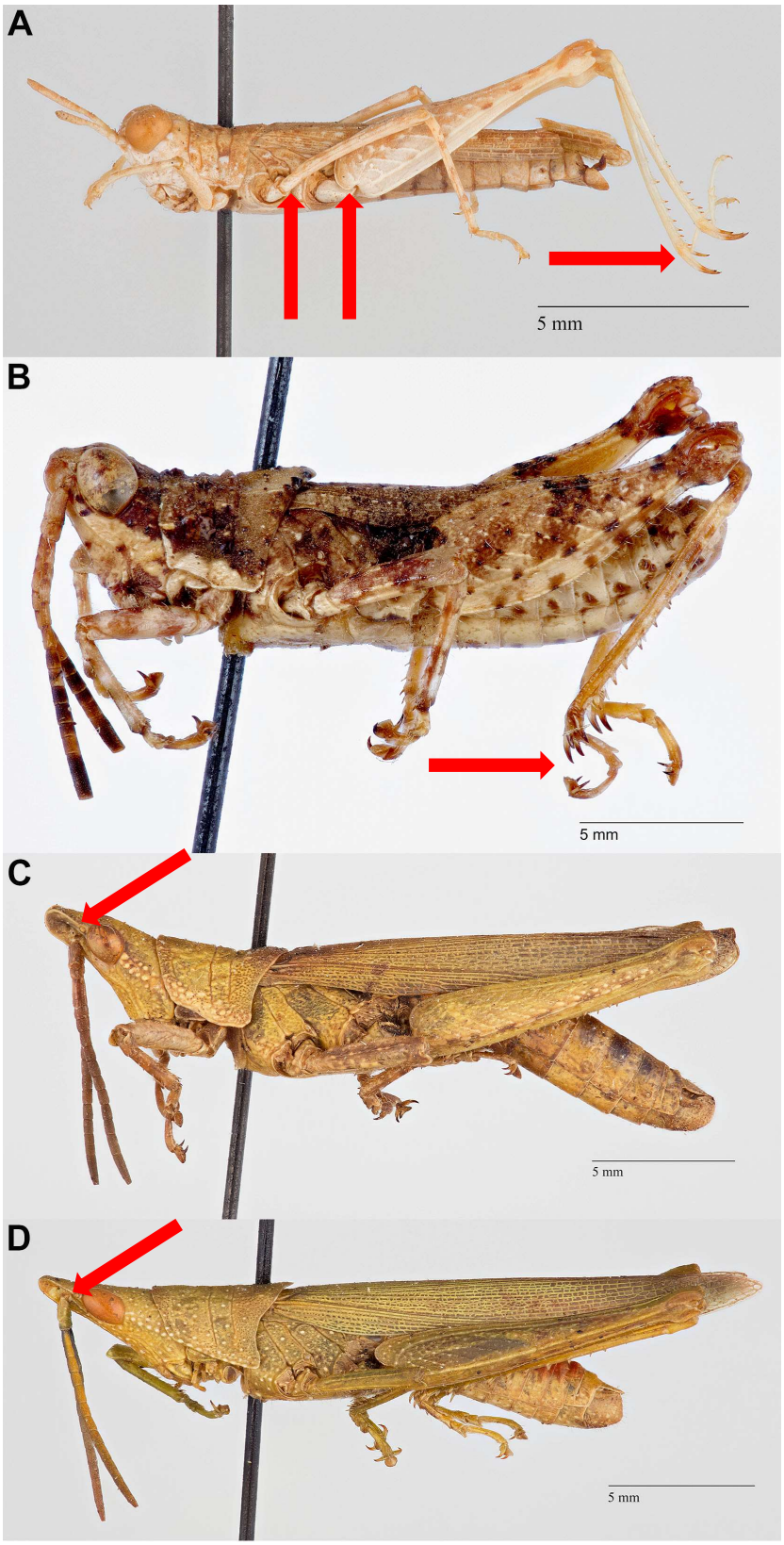

Figure 3.35. Western Asia Pyrgomorphidae. **A.** *Tenuitarsus angustus* male lateral view. **B.** *Chrotogonus trachypterus* male lateral view. **C.** *Pyrgomorpha viganudii* male lateral view. **D.** *Atractomorpha aberrans* male lateral view.

3.2.7 Key to Pyrgomorphidae genera of the Arabian Peninsula

According to Orthoptera Species File (Cigliano et al., 2018) this area corresponds to Gulf States, Kuwait, Oman, Saudi Arabia and Yemen (excluding Socotra Island). Nine genera, one endemic to the region.

1. Anterior margin of prosternum covering the posterior and lower part of the mouth (fig. 3.2E). 2

1'. Anterior margin of prosternum not covering the posterior and lower part of the mouth. 3

2. Spurs of hind tibia longer than the basal tarsal segment; middle femur thin and strongly elongated, as long as or longer than head and pronotum together; lower basal lobe of hind femur shorter than the upper one (fig. 3.36A). .....***Tenuitarsus*** **(1 sp.)**

(*T. angustus*)

2'. Spurs of hind tibia shorter than the basal tarsal segment; middle femur short, much shorter than head and pronotum together; lower basal lobe of hind femur longer than the upper one (fig. 3.36B). .....***Chrotogonus*** **(1 sp.)**

(*C. homalodemus*)

3. Fully winged. 4

3'. Tegmina vestigial. 6

4. Antennae base present below lateral ocelli. 5

4'. Antennae base present in front of lateral ocelli (fig. 3.36C). (Yemen) .....***Atractomorpha*** **(1 sp.)**

(*A. acutipennis*)

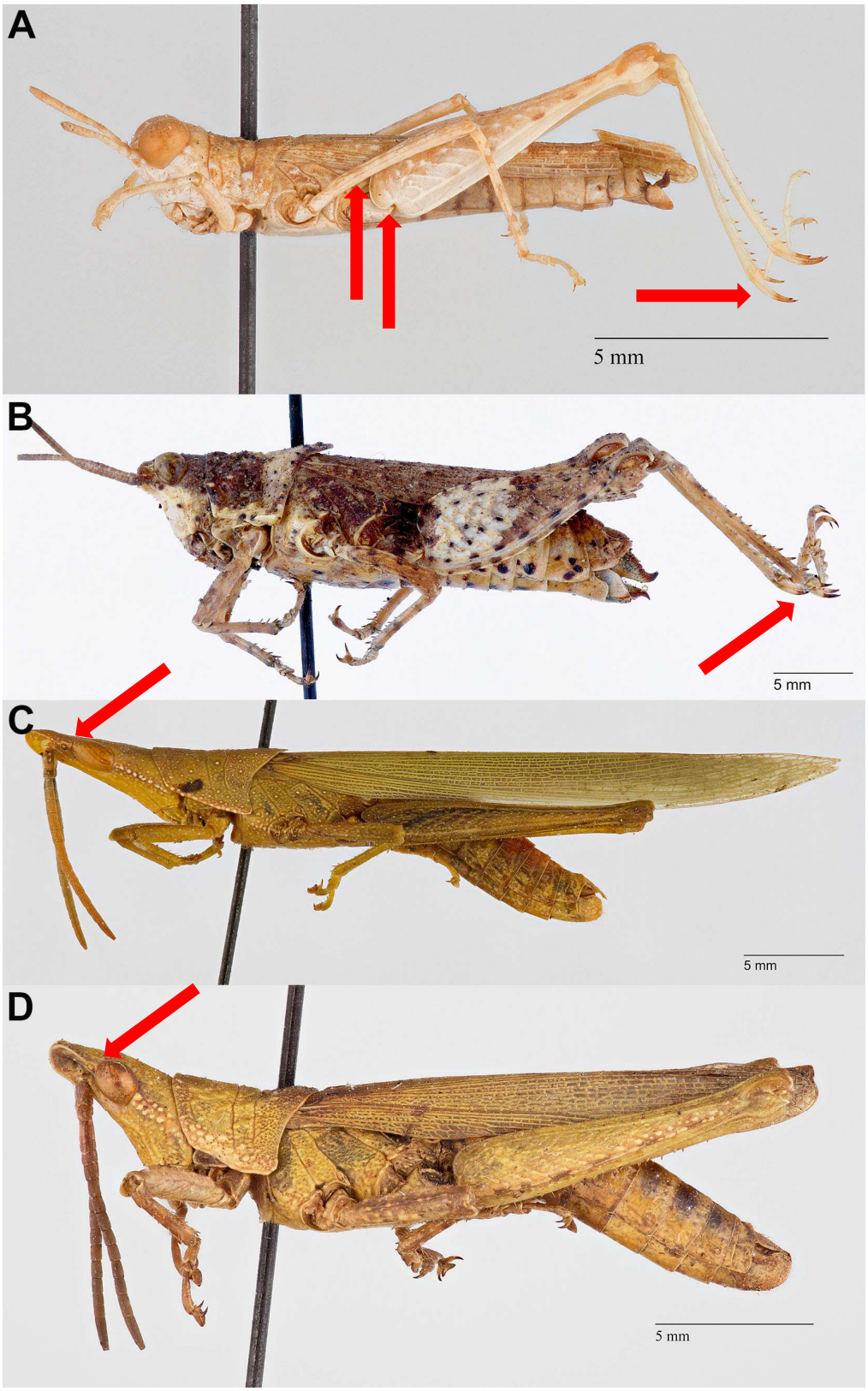

Figure 3.36. Arabian Peninsula Pyrgomorphidae 1. **A.** *Tenuitarsus angustus* male lateral view. **B.** *Chrotogonus homalodemus* male lateral view. **C.** *Pyrgomorpha viganudii* male lateral view. **D.** *Atractomorpha aberrans* male lateral view.

5. Row of tubercles running from eye to the lateral anterior margin of pronotum (fig. 3.36C).

.....***Pyrgomorpha* (2 spp.)**

(*P. conica, P. hemiptera*)

5'. No row of tubercles running from eye to the lateral anterior margin of pronotum (fig. 3.37A,B). .....***Poekilocerus* (2 spp.)**

(*P. arabicus, P. bufonius*)

6. Body with rugose texture. 7

6'. Body with smooth texture (fig. 3.38A). (Yemen) .....***Popovia** (1 sp.)**

(*P. salvadorae*)

7. Space between eye and lateral anterior margin of pronotum approximately the length of an eye. 8

7'. Space between eye and lateral anterior margin of pronotum less than the length of an eye (fig. 3.38B**)**. (Yemen) .....***Pyrgomorphellula* (1 sp.)**

(*P. curtula*)

8. Tegmina vestigial with no veins visible (fig. 3.38C). (Yemen) ……...***Parasphenula* (2 spp.)**

(*P. tewfiki, P. yemenita*)

8'. Tegmina tongue-like with some veins present (fig. 3.38D). (Saudi Arabia)

.....***Pyrgomorphella* (1 sp.)**

(*P. rotundata*)

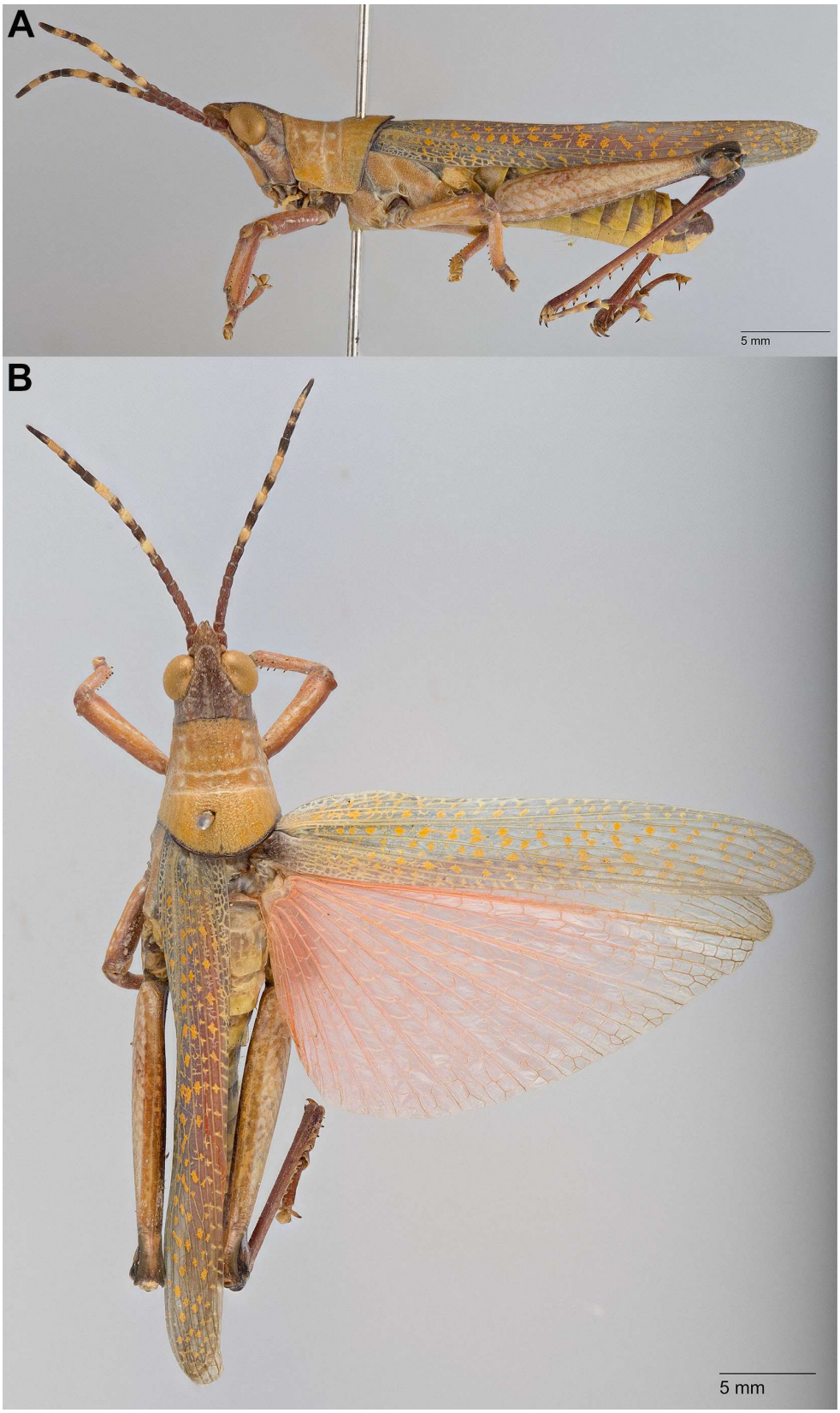

Figure 3.37. Arabian Peninsula Pyrgomorphidae 2. **A.** *Poekilocerus arabicus* male lateral view. **B.** *P. arabicus* male dorsal view.

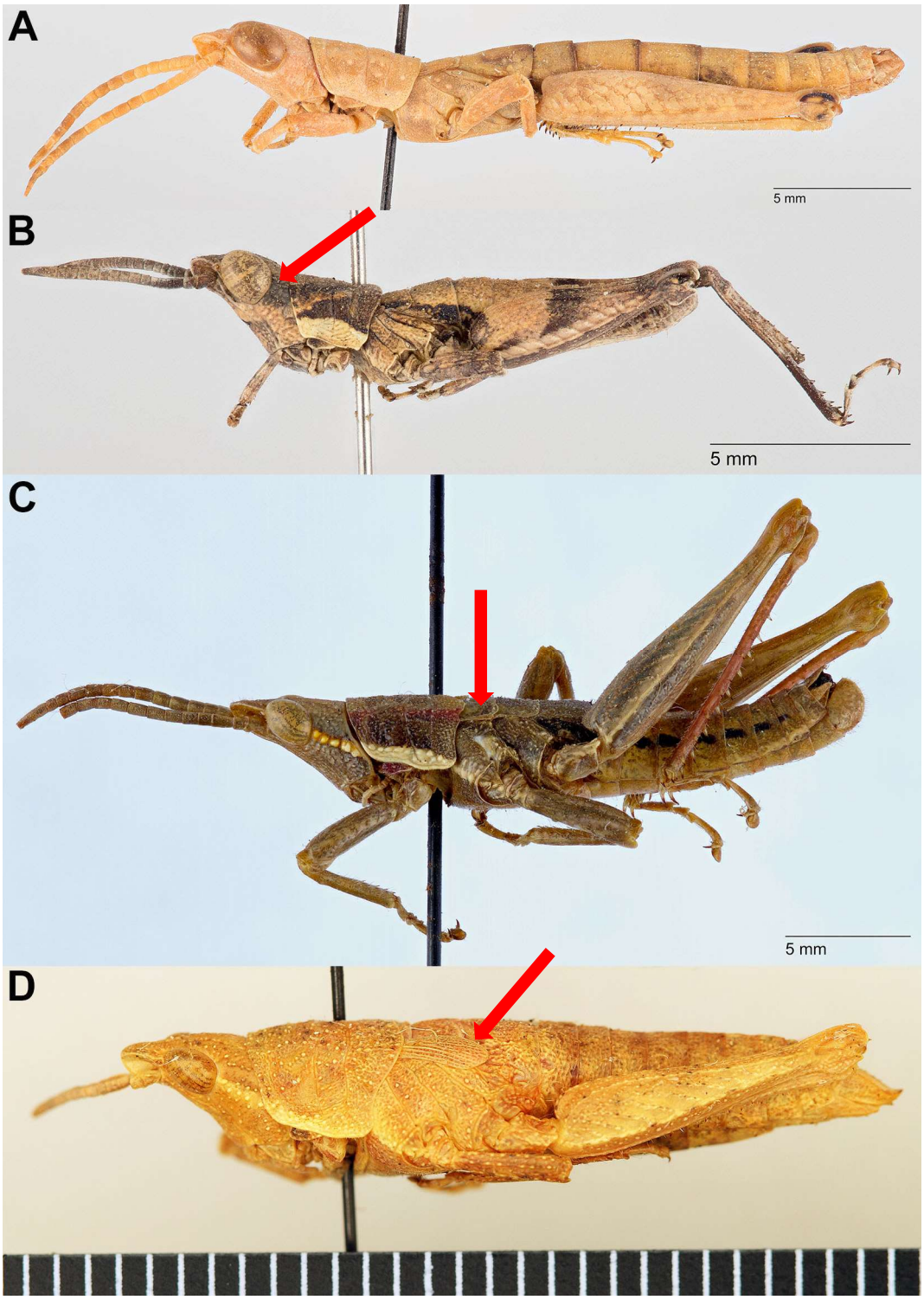

Figure 3.38. Arabian Peninsula Pyrgomorphidae 3. **A.** *Popovia salvadorae* male lateral view. **B.** *Pyrgomorphellula curtula* male lateral view. **C.** *Parasphenula yemenita* male lateral view. **D.** *Pyrgomorphella rotundata* female lateral view.

3.2.8 Key to Pyrgomorphidae genera of Indian Subcontinent

Some information from Kevan & Singh (1964), Kevan (1968), Schmidt (2004) and Shishodia et al. (2010).

According to Orthoptera Species File (Cigliano et al., 2018) this area corresponds to Bangladesh, India, Nepal, Pakistan, Sri Lanka and Bhutan

Twenty one genera, ten endemic to the region.

1. Anterior margin of prosternum covering the posterior and lower part of the mouth (fig. 3.2E). 2

1'. Anterior margin of prosternum not covering the posterior and lower part of the mouth. 3

2. Spurs of hind tibia longer than the basal tarsal segment; middle femur thin and strongly elongated, as long as or longer than head and pronotum together; lower basal lobe of hind femur shorter than the upper one (fig. 3.39A). .....***Tenuitarsus*** **(1 sp.)**

(*T. orientalis*)

2'. Spurs of hind tibia shorter than the basal tarsal segment; middle femur short, much shorter than head and pronotum together; lower basal lobe of hind femur longer than the upper one (fig. 3.39B). .....***Chrotogonus*** **(4 spp.)**

(*C. brachypterus, C. homalodemus, C. oxypterus, C. trachypterus*)

3. Apterous. 4

3'. Micropterous, brachypterous or fully winged. 9

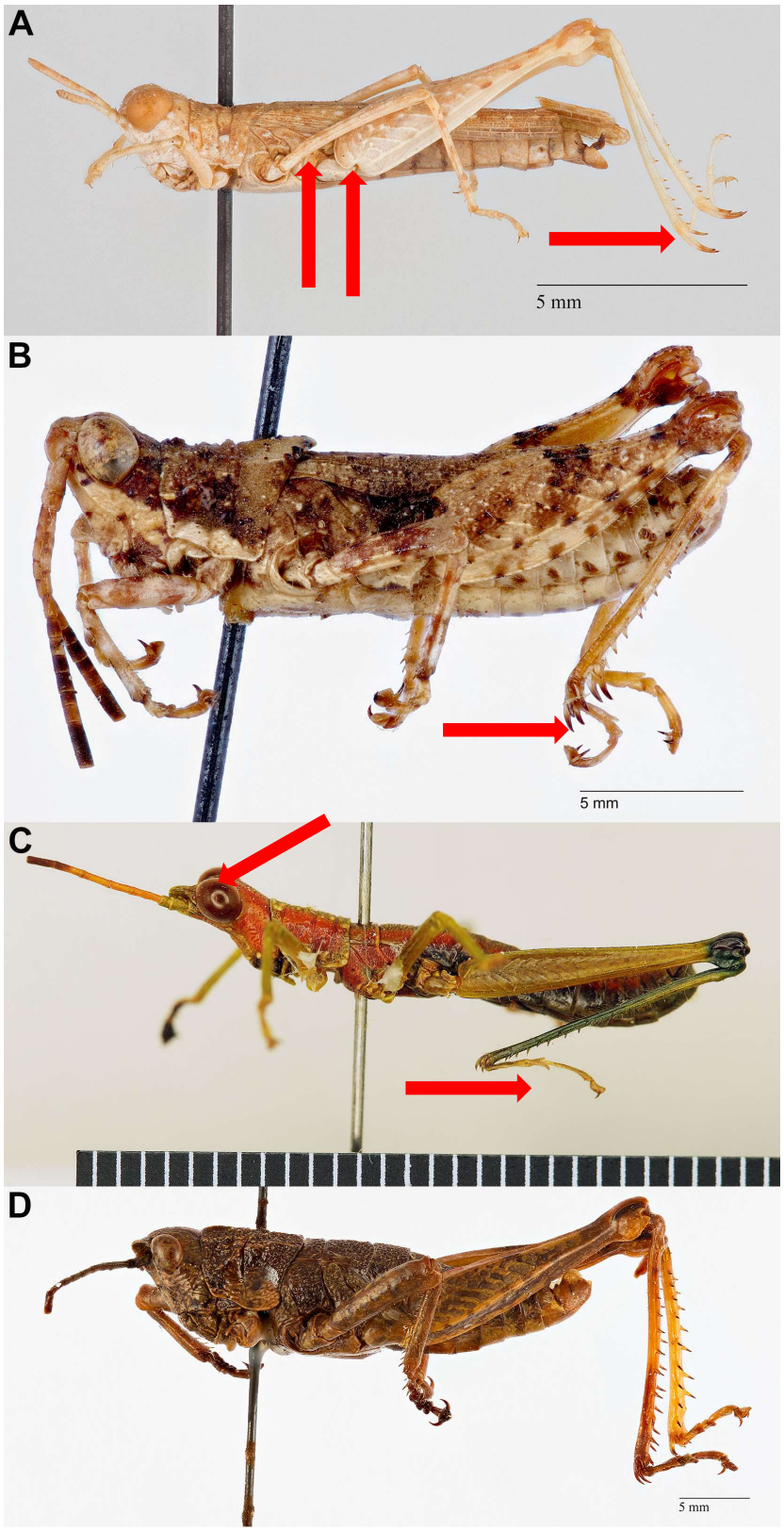

Figure 3.39. Indian Subcontinent Pyrgomorphidae 1. **A.** *Tenuitarsus angustus* male lateral view. **B.** *Chrotogonus trachypterus* male lateral view. **C.** *Rakwana ornata* male lateral view. **D.** *Mekongiella kingdoni* male lateral view.

4. Spherical eyes, very prominent; hind leg, third tarsomere longer than first tarsomere (fig. 3.39C). (Sri Lanka) .....***Rakwana**** **(1 sp.)**

(*R. ornata*)

4'. Not spherical eyes, no prominent; hind leg, third tarsomere no longer than first tarsomere. 5

5. Body robust (fig. 3.39D). (Arunachal Pradesh) .....***Mekongiella*** **(1 sp.)**

(*M. wardi*)

5'. Body slender. ……...6

6. Space between eye and anterior margin of pronotum in lateral view with a row of tubercles (fig. 3.40A). (Tamil Nadu) .....***Anarchita**** **(1 sp.)**

(*A. aptera*)

6'. Space between eye and anterior margin of pronotum in lateral view without a row of tubercles. 7

7. Antennae longer than head and pronotum together. 8

7'. Antennae shorter than head and pronotum together (fig. 3.40B). (Tamil Nadu). .....***Nilgiracris**** **(1 sp.)**

(*N. raoi*)

8. Body cylindrical; head slightly longer than its width; extremely elongate, whip-like aedegal sclerites (fig. 3.40C). (Andhra Pradesh, Tamil Nadu, Kerala). ……..……***Neorthacris**** **(5 spp.)**

(*N. acuticeps, N. longicercata, N. malabarensis, N. palnensis, N. simulans*)

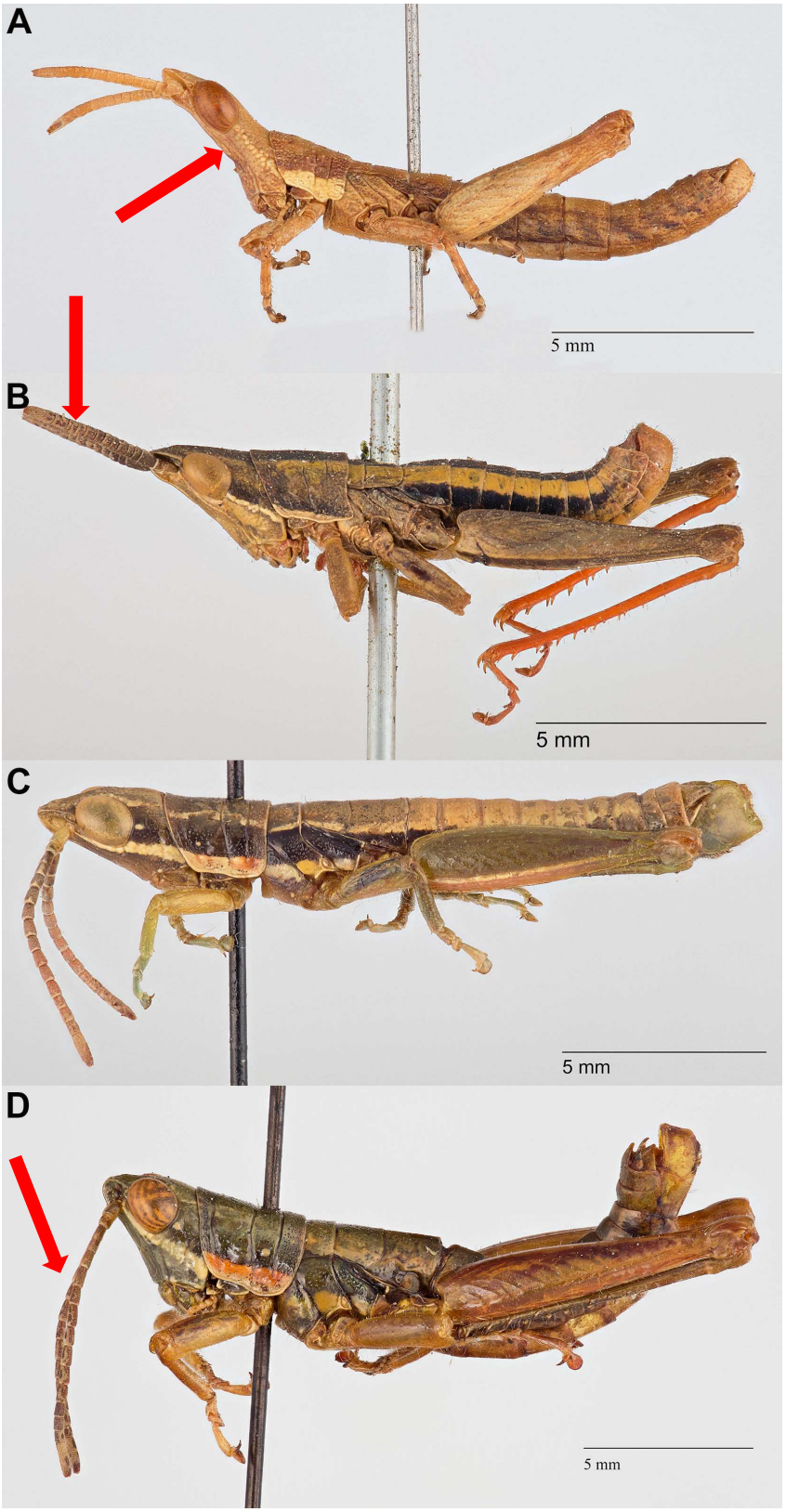

Figure 3.40. Indian Subcontinent Pyrgomorphidae 2. **A.** *Anarchita aptera* male lateral view. **B.** *Nilgiracris raoi* male lateral view. **C.** *Neorthacris acuticeps* male lateral view. **D.** *Orthacris incongruens* male lateral view.

8’. Body varying from cylindrical to rather robust, subfusiform; head variable in form but frequently not longer than its width or shorter; aedagal sclerites normal (fig. 3.40D). (Tamil Nadu, Sri Lanka) .....***Orthacris**** **(13 spp.)**

(*O. ceylonica, O. comorensis, O. curvicerca, O. elongata, O. filiformis, O. gracilis, O. maindroni, O. major, O. elegans, O. incongruens, O. ramakrishnai. O. robusta, O ruficornis*)

9. Micropterous. 10

9’. Brachypterous or tegmina fully developed. 11

10. Small eyes (1/4 of total length of head in lateral view) (fig. 3.41A). (Andhra Pradesh, Karnataka, Maharashtra, Tamil Nadu) ……..……***Colemania**** **(1 sp.)**

(*C. sphenarioides*)

10’. Medium eyes (1/3 of total length of head in lateral view) (fig. 3.41B). (Karnataka)

.....***Ramakrishnaia**** **(2 spp.)**

(*R. gracilis, R. notabilis*)

11. Brachypterous. 12

11’. Tegmina fully developed. 15

12. A row of tubercles running from eye to pronotum present in lateral view. 13

12’. Such a row of tubercles absent. 14

13. Tegmina reaching one third of hind femur from the base. The length of a row of tubercles similar to the length of eye in lateral view (fig. 3.41C). (India) .....***Zarytes**** **(1 sp.)**

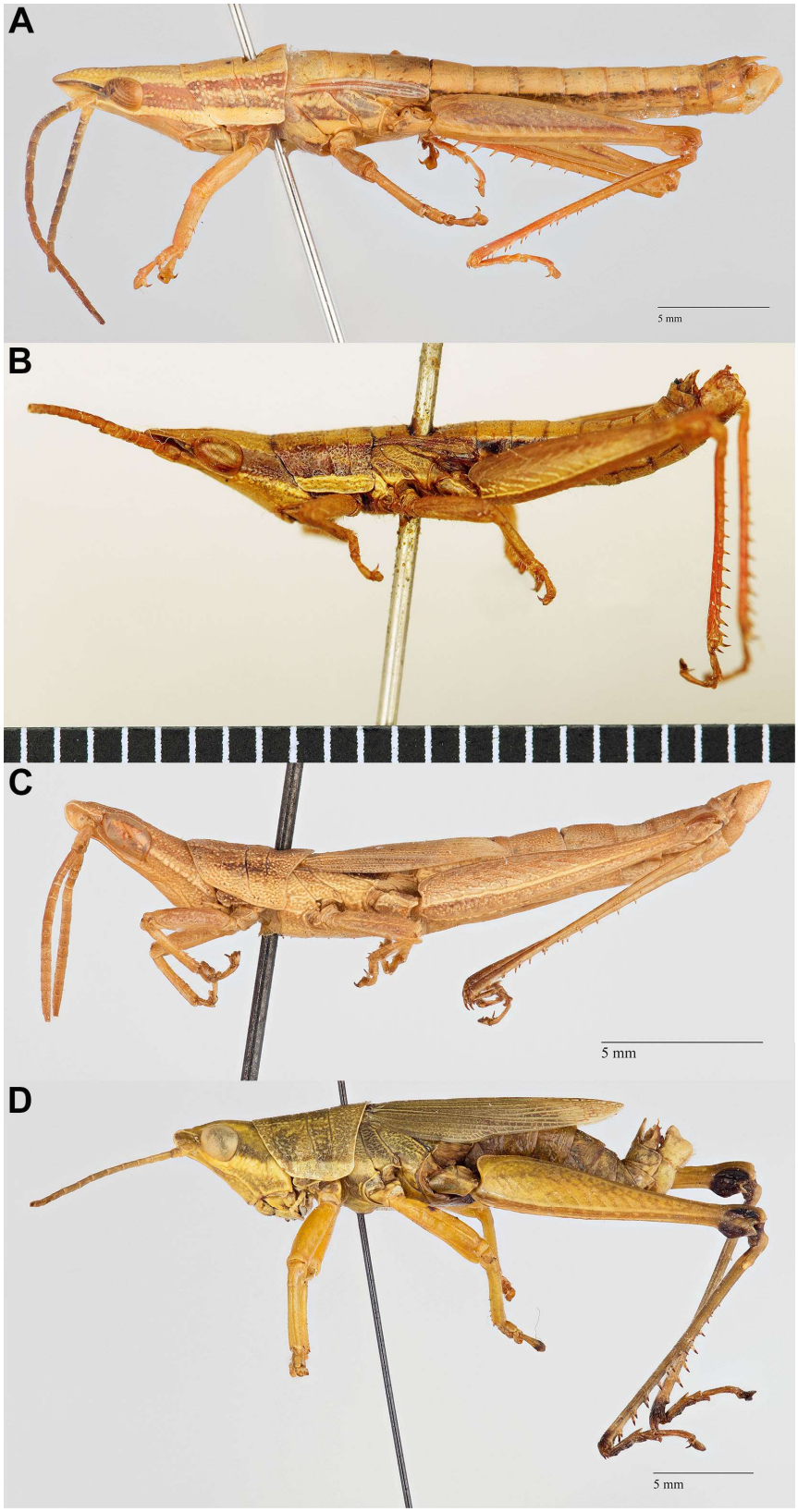

Figure 3.41. Indian Subcontinent Pyrgomorphidae 3. **A.** *Colemania sphenarioides* male lateral view. **B.** *Ramakrishnaia gracilis* male lateral view. **C.** *Zarytes squalinus* male lateral view. **D.** *Chlorizeina unicolor* male lateral view.

(*Z. squalinus*)

13’. Tegmina barely reaching hind femur. The length of a row of tubercles twice the length of eye in lateral view. (Tamil Nadu) .....***Plerisca*** **(1 sp.)**

(*P. sudindica*)

14. Body distinctly fusiform. Head distinctly conical, eyes not prominent. (Goa, Karnataka, Maharashtra) .....***Feacris**** **(2 spp.)**

(*F. malabarensis, F. reducta*)

14’. Body subfusiform. Head conical, eyes rather prominent (fig. 3.41D). (Assam, Manipur, Tripura, Sri Lanka). ….....***Chlorizeina*** **(1 sp.)**

(*C. unicolor*)

15. Pronotum unarmed without a bilobed tubercle nor spines in prozona. 16

15’. Pronotum with a bilobed tubercle and spines in prozona (fig. 3.42A). (India, Bangladesh, Nepal, Pakistan, Sri Lanka) .....***Aularches*** **(1 sp.)**

(*A. miliaris*)

16. Antennae base present in front of lateral ocelli. 17

16’. Antennae base present below lateral ocelli. 19

17. Marginal area of hind femur not expanded, narrower than medial area; cerci straight. 18

17’. Marginal area of hind femur expanded, as wide as medial area; cerci bent (fig. 3.42B). (India, Bangladesh) .....***Pseudomorphacris*** **(1 sp.)**

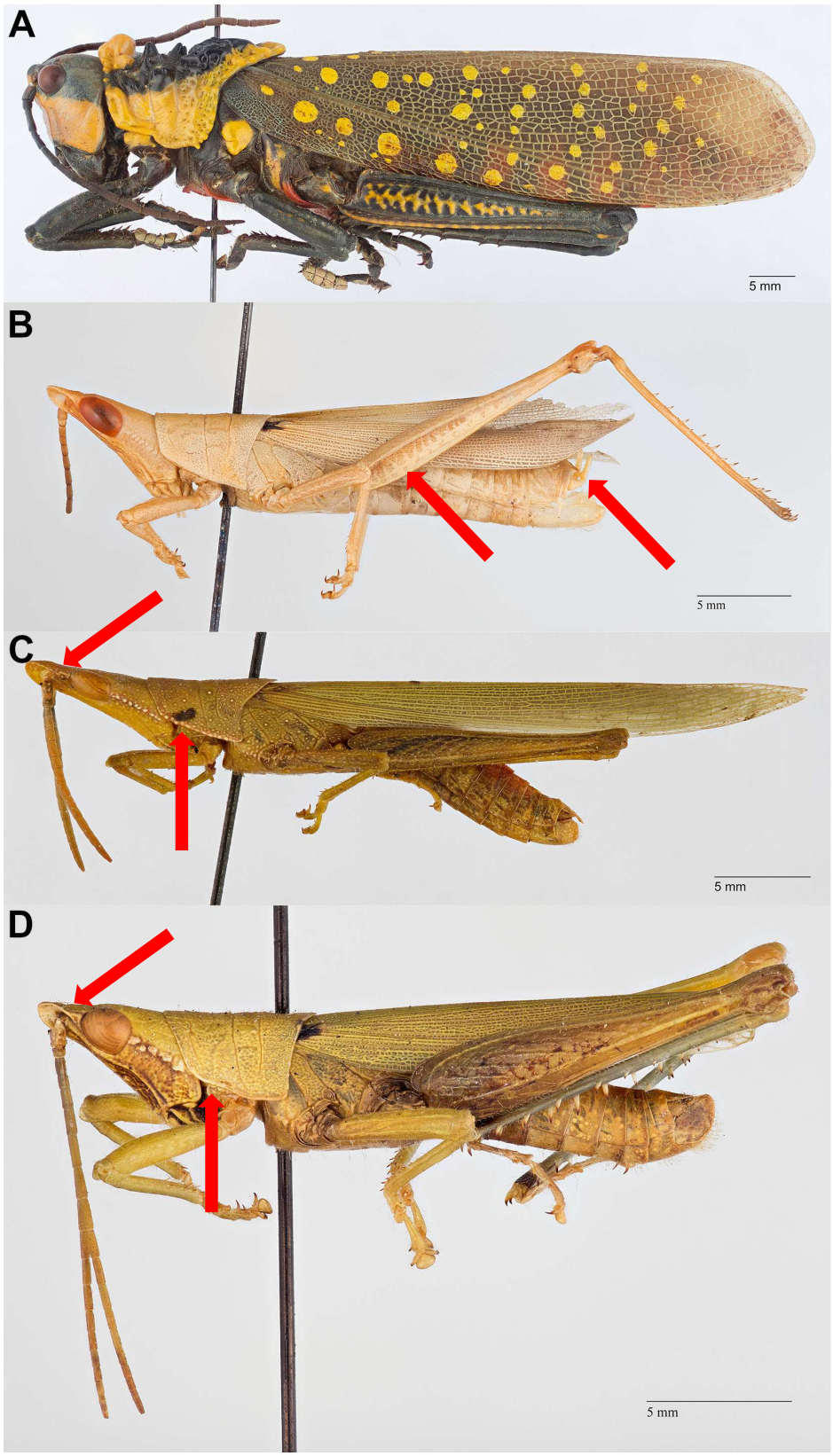

Figure 3.42. Indian Subcontinent Pyrgomorphidae 4. **A.** *Aularches miliaris* male lateral view. **B.** *Pseudomorphacris notata* male lateral view. **C.** *Atractomorpha acutipennis* male lateral view. **D.** *Tagasta indica* male lateral view.

(*P. notata*)

18. Lateral margin of pronotum with a row of tubercles, continuing from head (fig. 3.42C).

.....***Atractomorpha*** **(7 spp.)**

(*A. acutipennis, A. angusta, A. burri, A. crenulata, A. himalayica, A. psittacina, A. sinensis*)

18'. Lateral margin of pronotum without a row of tubercles (fig. 3.42D). (India, Buthan, Nepal). ……....……...***Tagasta*** **(3 spp.)**

(*T. indica, T. longipenne, T. marginella*)

19. A row of tubercles running from the eye to pronotum absent in lateral view. 20

19'. A row of tubercles running from the eye to pronotum present in lateral view (fig. 3.43A).

.....***Pyrgomorpha*** **(3 spp.)**

(*P. bispinosa, P. conica, P. inaequalipennis*)

20. Radial sector in tegmina well developed. Large in size (5-6 cm) (fig. 3.43B). (India, Pakistan, Nepal) .....***Poekilocerus*** **(2 spp.)**

(*P. geniplanus, P. pictus*)

20'. Radial sector in tegmina poorly developed. Small in size (2-3 cm) (fig. 3.43C). (Bihar)

.....***Pterorthacris**** **(1 sp.)**

(*P. subcallosa*)

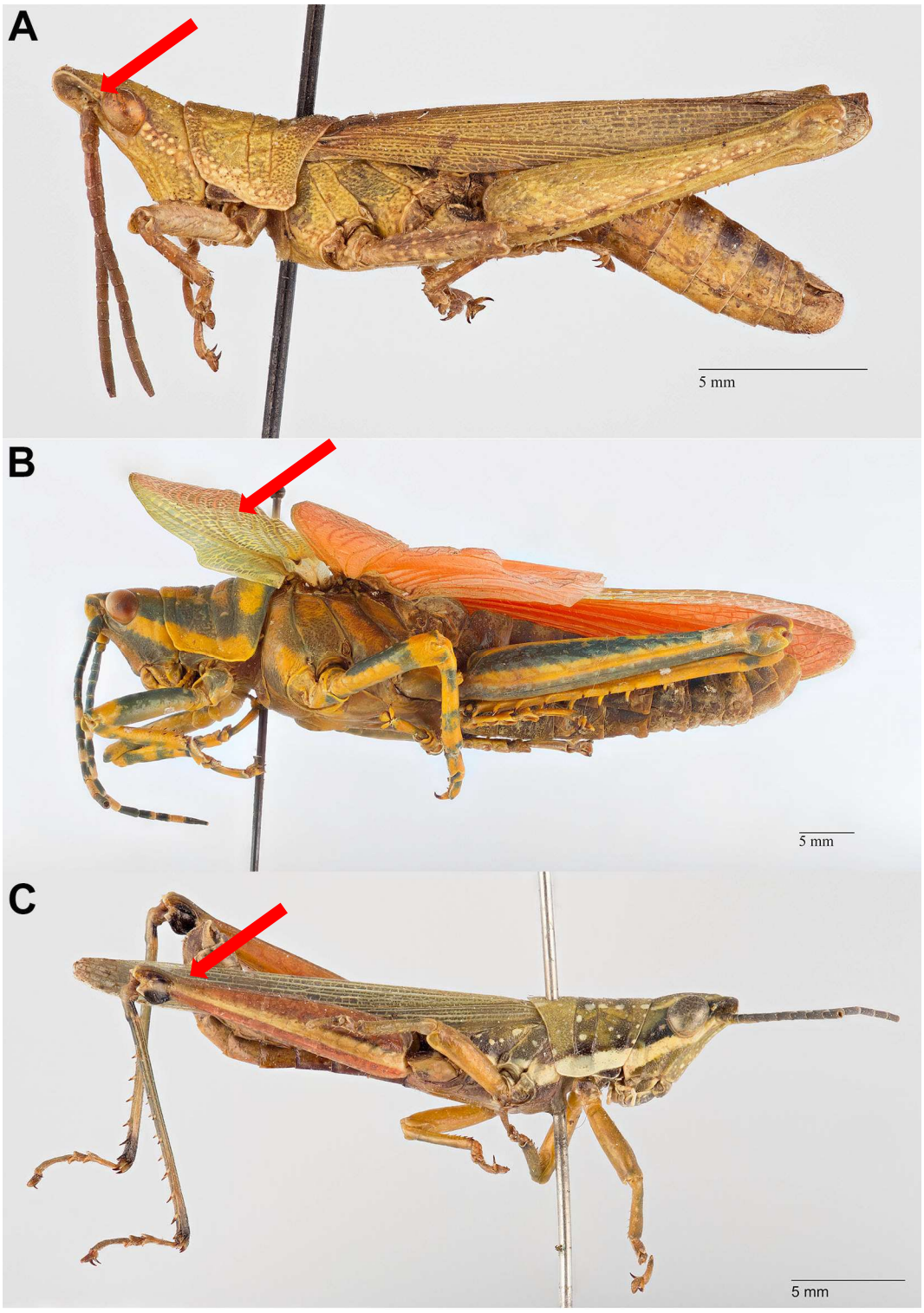

Figure 3.43. Indian Subcontinent Pyrgomorphidae 5. **A.** *Pyrgomorpha vignaudii* male lateral view. **B.** *Poekilocerus pictus* male lateral view. **C.** *Pterorthacris subcallosa* male lateral view.

3.2.9 Key to Pyrgomorphidae genera of Southeast Asia

According to Orthoptera Species File (Cigliano et al., 2018) this area corresponds to Cambodia, Laos, Myanmar, Thailand and Vietnam.

Nine genera, three endemic to the region.

1. Tegmina absent. 2

1'. Tegmina present. 3

2. Fastigium of vertex well developed; head elongated (fig. 3.44A). (Cambodia)

.....***Arbuscula**** **(1 sp.)**

(*A. cambodjiana*)

2'. Fastigium of vertex poorly developed; head short (fig. 3.44B). (Vietnam)

.....***Kuantania*** **(1 sp.)**

(*K. aptera*)

3. Antennae base present below lateral ocelli. 4

3'. Antennae base present in front of lateral ocelli. 7

4. Pronotum with tubercles and spines (fig. 3.42A). .....***Aularches*** **(1 sp.)**

(*A. miliaris*)

4'. Pronotum without tubercles and spines. 5

5. Tegmina brachypterous. ……...6

5'. Tegmina vestigial (fig. 3.44C). (Myanmar) .....***Burmorthacris**** **(1 sp.)**

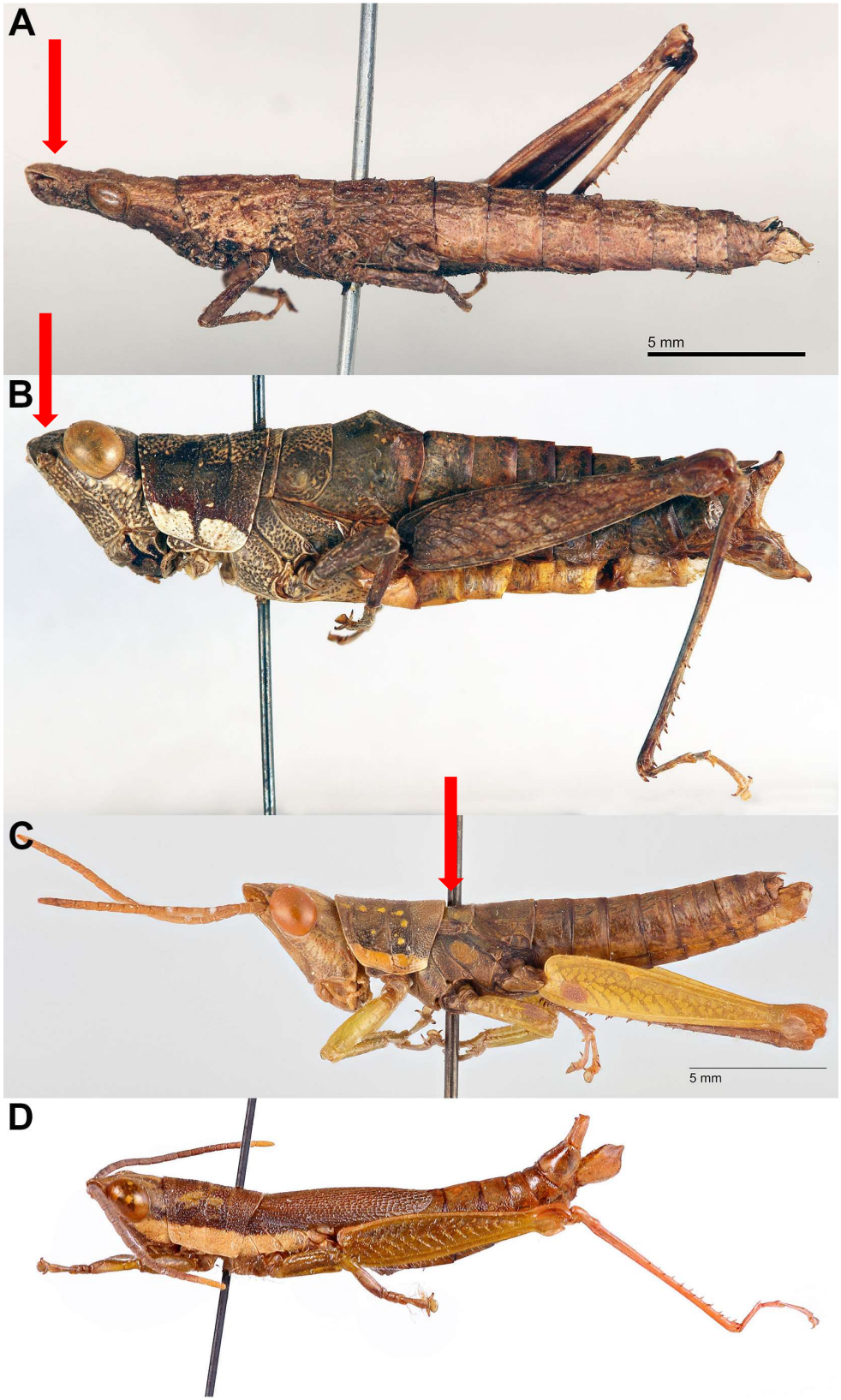

Figure 3.44. Southeast Asia Pyrgomorphidae 1. **A.** *Arbuscula cambodjiana* female lateral view. **B.** *Kuantanaia aptera* female lateral view. **C.** *Burmorthacris subaptera* male lateral view. **D.** *Megradina festiva* male lateral view.

6. Body subfusiform; hind femur longer than the length of abdomen (fig. 3.41D).

.....***Chlorizeina*** **(3 spp.)**

(*C. feae, C. togulata, C. unicolor*)

6’. Body cylindrical; hind femur shorter than the length of abdomen (fig. 3.44D). (Vietnam)

.....***Megradina**** **(1 sp.)**

(*M. festiva*)

7. Marginal area of hind femur not expanded, narrower than medial area; cerci straight.

.....8

7’. Marginal area of hind femur expanded, as wide as medial area; cerci bent (fig. 3.42B).

.....***Pseudomorphacris*** **(3 spp.)**

(*P. brachyptera, P. hollisi, P. notata*)

8. A row of tubercles from eye continuing to the lateral margin of pronotum (fig. 3.42C).

.....***Atractomorpha*** **(6 spp.)**

(*A. angusta, A. burri, A. crenulata, A. lata, A. psittacina, A. sinensis*)

8’. A row of tubercles from eye not continuing to the lateral margin of pronotum (fig. 3.42D).

.....***Tagasta*** **(3 spp.)**

(*T. indica, T. marginella, T. tonkinensis*)

3.2.10 Key to Pyrgomorphidae genera of Malesia

With some information from Kevan (1963).

According to Orthoptera Species File (Cigliano et al., 2018) this area corresponds to Malaysia, Philippines, Indonesia (except for New Guinea Island)

Fourteen genera, eight endemic to the region.

1. Body laterally compressed. 2

1'. Body not laterally compressed. 5

2. Space between eye and pronotum in lateral approximately the length of eye. 3

2'. Space between eye and pronotum in lateral view twice the length of eye (fig. 3.45A). (Philippines) .....***Brunniella**** **(1 sp.)**

(*B. antistes*)

3. Tegmina with a distinct apical point about or in advance of the middle of the apical margin; one species brachypterous (fig. 3.45B). (Philippines) ……..***Apodesmoptera**** **(3 spp.)**

(*A. curtipennis, A. mira, A. luzonica*)

3'. Tegmina with a distinct apical point distinctly nearer the posterior than the anterior margin of tegmina. 4

4. Tegmina not tapering from near the base, anterior margin usually curving rather abruptly into apical margin; medium size, more than 22 mm for males and 33 mm for females (fig. 3.45C). .....***Desmoptera*** **(3 spp.)**

(*D. judicata, D. novaeguineae, D. degenerata*)

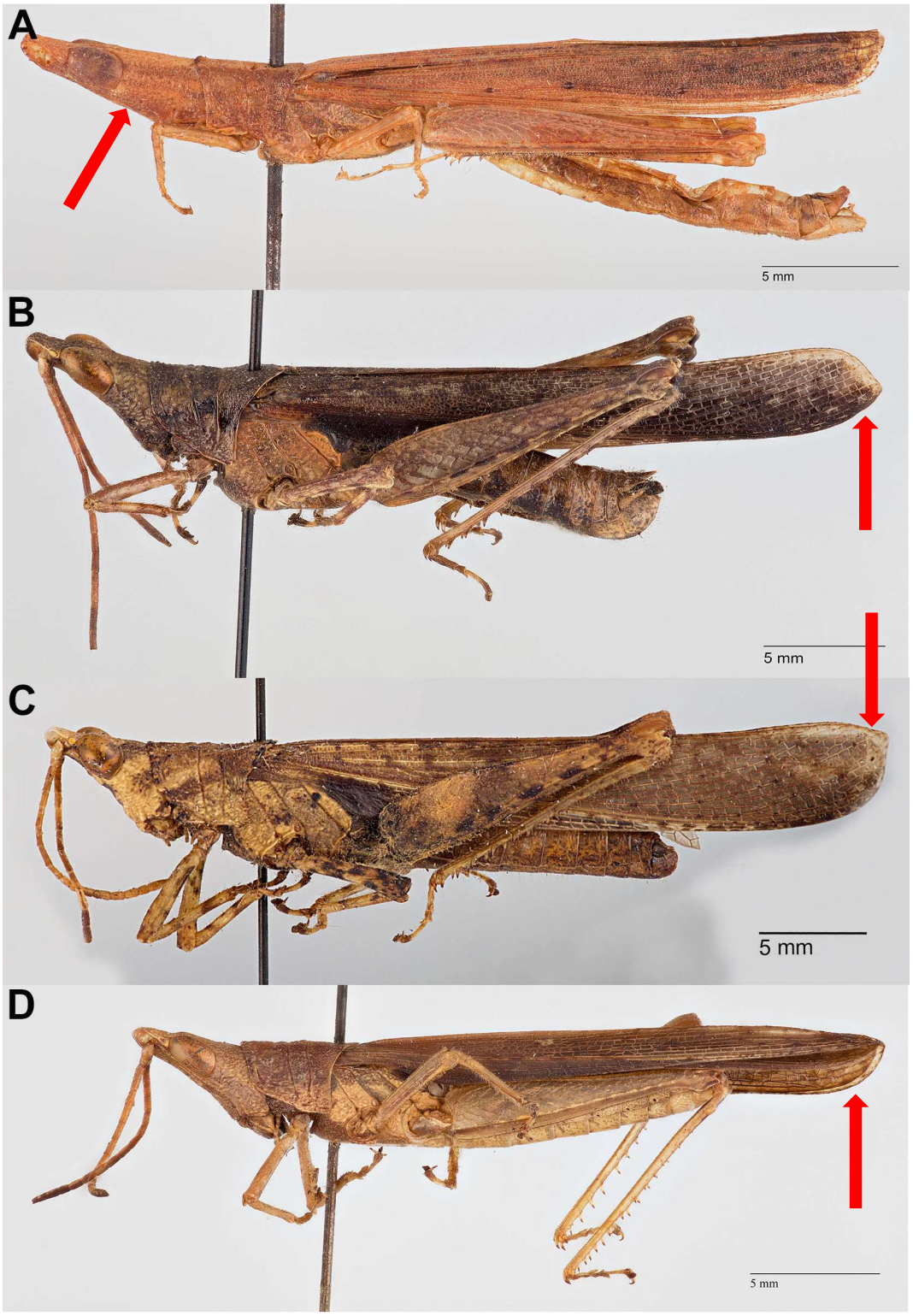

Figure 3.45. Malesia Pyrgomorphidae 1. **A.** *Bruniella antistes* male lateral view. **B.** *Apodesmoptera mira* male lateral view. **C.** *Desmoptera novaeguineae* male lateral view. **D.** *Desmopterella angustata* male lateral view.

4’. Tegmina often tapering gradually from near the base, anterior margin curving more gradually into the apical margin; small size, less than 22 mm for males and 35 for females (fig. 3.45D). .....***Desmopterella*** **(2 spp.)**

(*D. keyensis, D. sundaica*)

5. Tegmina present. 6

5’. Apterous (fig. 3.46A). (Philippines) .....***Philippyrgus****** **(1 sp.)**

(*P. subapterus*)

6. Micropterous. ……7

6’. Brachypterous or macropterous. 8

7. Head smooth; antennae much longer than head and pronotum together (fig. 3.46B). (Philippines) .....***Meubelia****** **(7 spp.)**

(*M. atriantennis, M. bakeri, M. bivittata, M. bruneri, M. gracilis, M. leytensis, M. schistacra*)

7’. Head foveolate; antennae around the length of head and pronotum together (fig. 3.46C). (Malaysia) .....***Kuantania*** **(1 sp.)**

(*K. squamipennis*)

8. Brachypterous. 9

8’. Macropterous. 11

9. Head normal; hind tarsomeres short, not as long as half the length of hind tibia; last abdominal segment protruding. 10

Figure 3.46. Malesia Pyrgomorphidae 2. **A.** *Philipyrgus subapterus* male lateral view. **B.** *Meubelia leytensis* male lateral view. **C.** *Kuantania squamipennis* female lateral view. **D.** *Spinacris inermis* male lateral view.

9’. Head short; hind tarsomeres as long as half the length of hind tibia; last abdominal segment not protruding (fig. 3.46D). (Philippines) .....***Spinacris**** **(3 spp.)**

(*S. elegans, S. inermis, S. viridis*)

10. Fastigium of vertex short, not longer than its width; last abdominal segment in males with broad, simple, subcircular or semicircular posterior excision; cerci simple, elongate, evenly curved inwards and acute apically (fig. 3.47A,B). (Malay Peninsula, Borneo Island) .....***Mitricephaloides**** **(2 spp.)**

(*M. rhodopterus, M. rubrosignatus*)

10’. Fastigum of vertex longer, at least as long as wide; last abdominal segment with a deep narrow, elongate, oblong or key-hole shape posterior excision having thickened lateral margins; cerci robust, flattened, rather abruptly curved inwards towards the apices, which are blunt or truncated (fig. 3.47C,D). (Malay Peninsula, Sumatra Island, Java Island) .....***Mitricephala**** **(5 spp.)**

(*M. dohrni, M. javanica, M. milleri, M. vittata*)

11. A row of tubercles running from eye to pronotum in lateral view. 12

11’. Absence of such a row of tubercles. 13

12. A row of tubercles from eye continuing to the lateral margin of pronotum (fig. 3.42C). .....***Atractomorpha*** **(5 spp.)**

(*A. angusta, A. burri, A. psittacina, A. rhodoptera, A.similis*)

12’. A row of tubercles from eye not continuing to the lateral margin of pronotum (fig. 3.42D). .....***Tagasta*** **(7 spp.)**

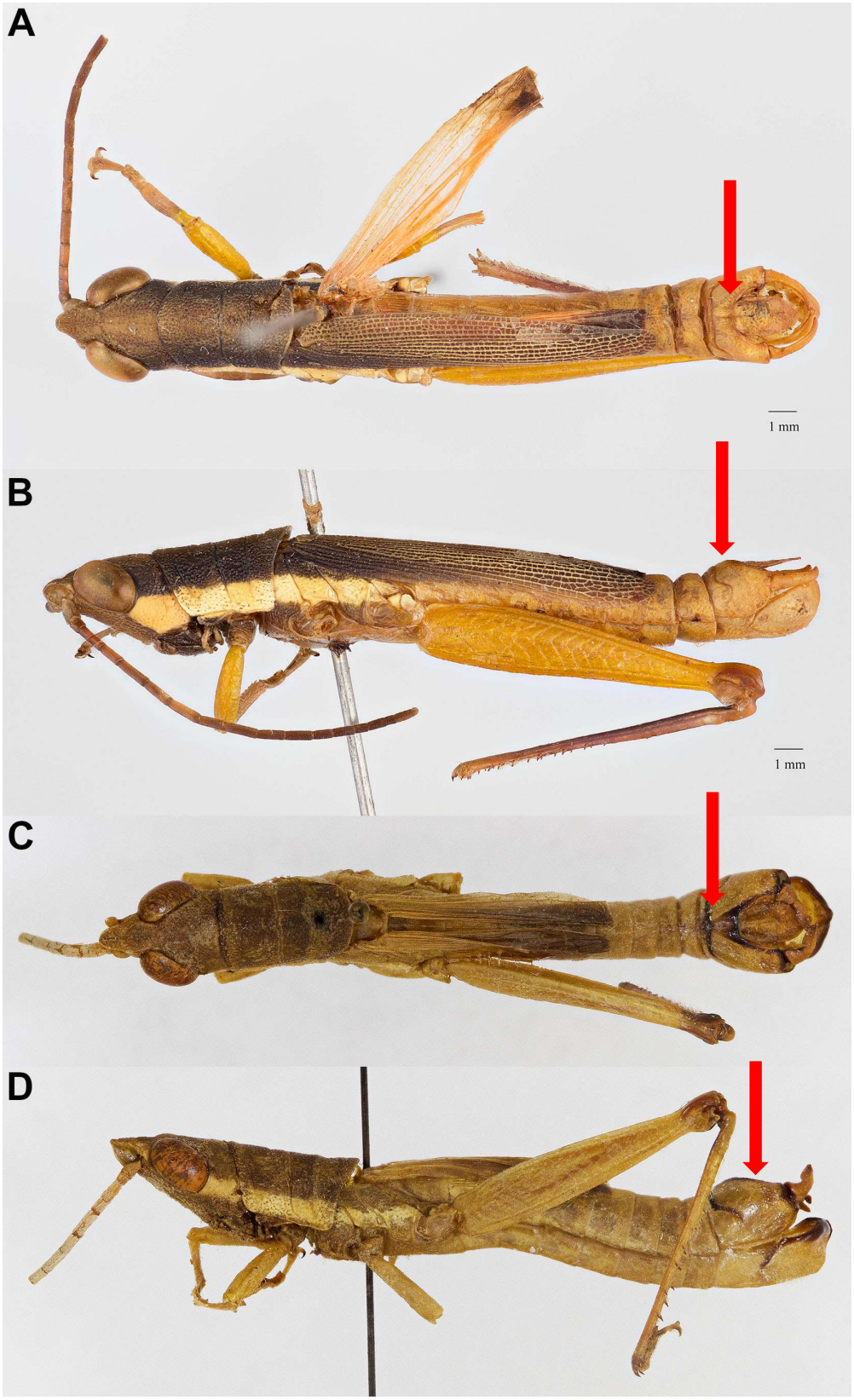

Figure 3.47. Malesia Pyrgomorphidae 3. **A.** *Mitricephaloides rhodopterus* male dorsal view. **B.** *M. rhodopterus* male lateral view. **C.** *Mitricephala javanica* male dorsal view. **D.** *M. javanica* male lateral view.

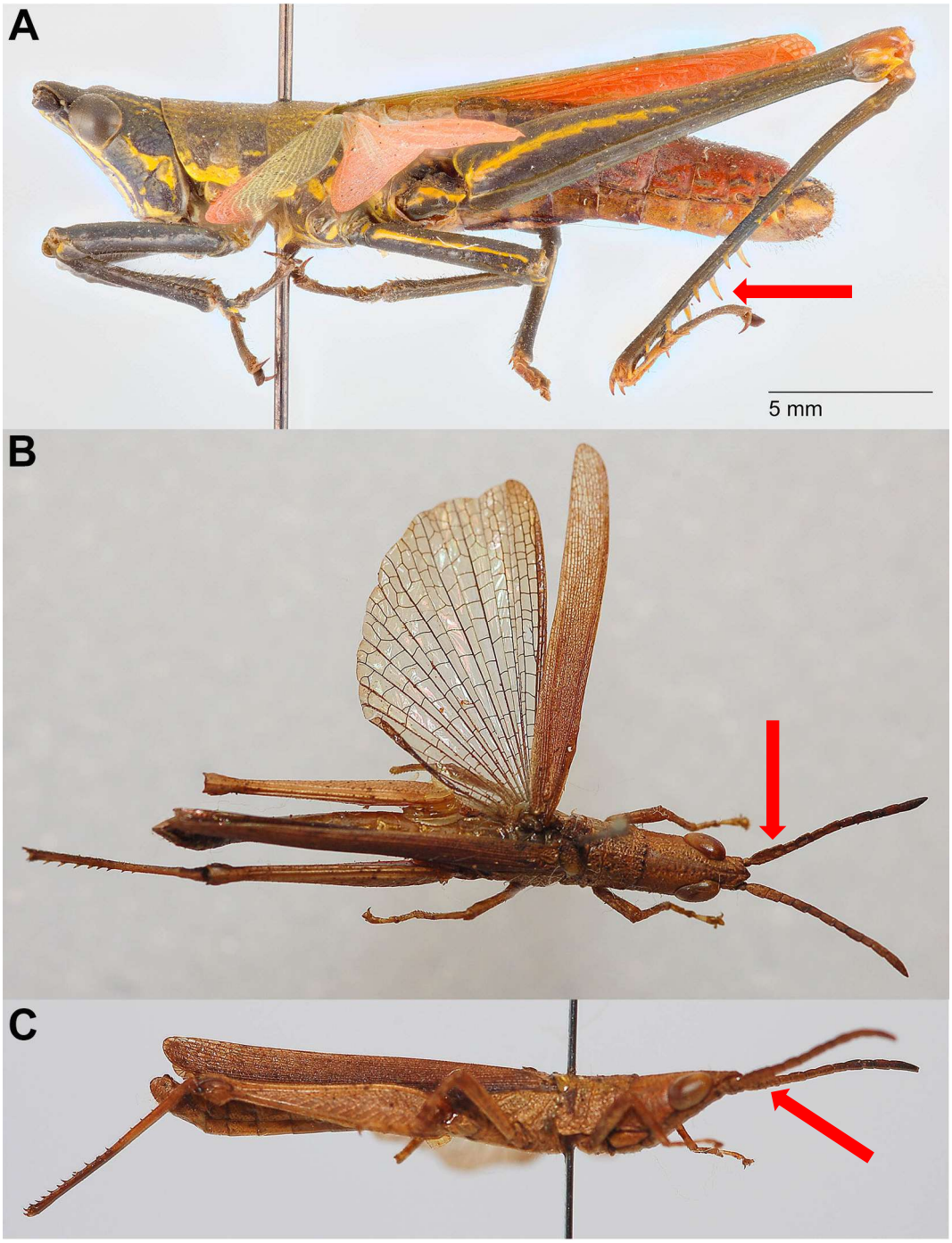

Figure 3.48. Malesia Pyrgomorphidae 4. **A.** *Annandalea haemoptera* male lateral view. **B.** *Verdulia subcycloidea* male dorsal view. **C.** *V. subcycloidea* male lateral view.

(*T. anoplosterna, T. celebesica, T. hoplosterna, T. inornata, T. insularis, T. marginella, T. striatipennis*)

13. Large spines on hind tibia, antennae filiform (fig. 3.48A). (Malay Peninsula, Java Island) ……..…….……...***Annandalea**** **(2 spp.)**

(*A. haematoptera, A. robinsoni*)

13’. Small spines on hind tibia, antennae serrated (fig. 3.48B,C). (Borneo Island) .....***Verdulia*** **(1 sp.)**

(*V. subcycloidea*)

3.2.11 Key to Pyrgomorphidae genera of Papuasia and Pacific Islands

This region is comprised of New Guinea Island (half left is Indonesia, half right is Papua New Guinea), Solomon Islands, Bismarck Archipelago, New Caledonia and Fiji Islands.

Twenty one genera, seventeen endemic to the region. *Atractomorpha sinensis* has been introduced in the Hawaiian Islands (Kevan, 1966).

Modified from Kevan (1963, 1966).

1. Body not laterally compressed. 2

1'. Body laterally compressed. 13

2. Absence of a row of tubercles running from eye to pronotum from lateral view. 3

2'. Presence of a row of tubercles running from eye to pronotum from lateral view (fig. 3.42C). (New Guinea Island) .....***Atractomorpha*** **(1 sp.)**

(*A. crenaticeps*)

3. Eyes small, covering less than half of total head length in lateral view. 4

3'. Eyes large, almost always covering more than half of total head length in lateral view. 5

4. Antennae serrated, shorter than head and thorax together (fig. 3.49A,B). (New Guinea Island) .....***Verdulia*** **(1 sp.)**

(*V. cycloidea*)

4'. Antennae filiform, longer than head and thorax together. (Fiji Islands) .....***Fijipyrgus**** **(1 sp.)**

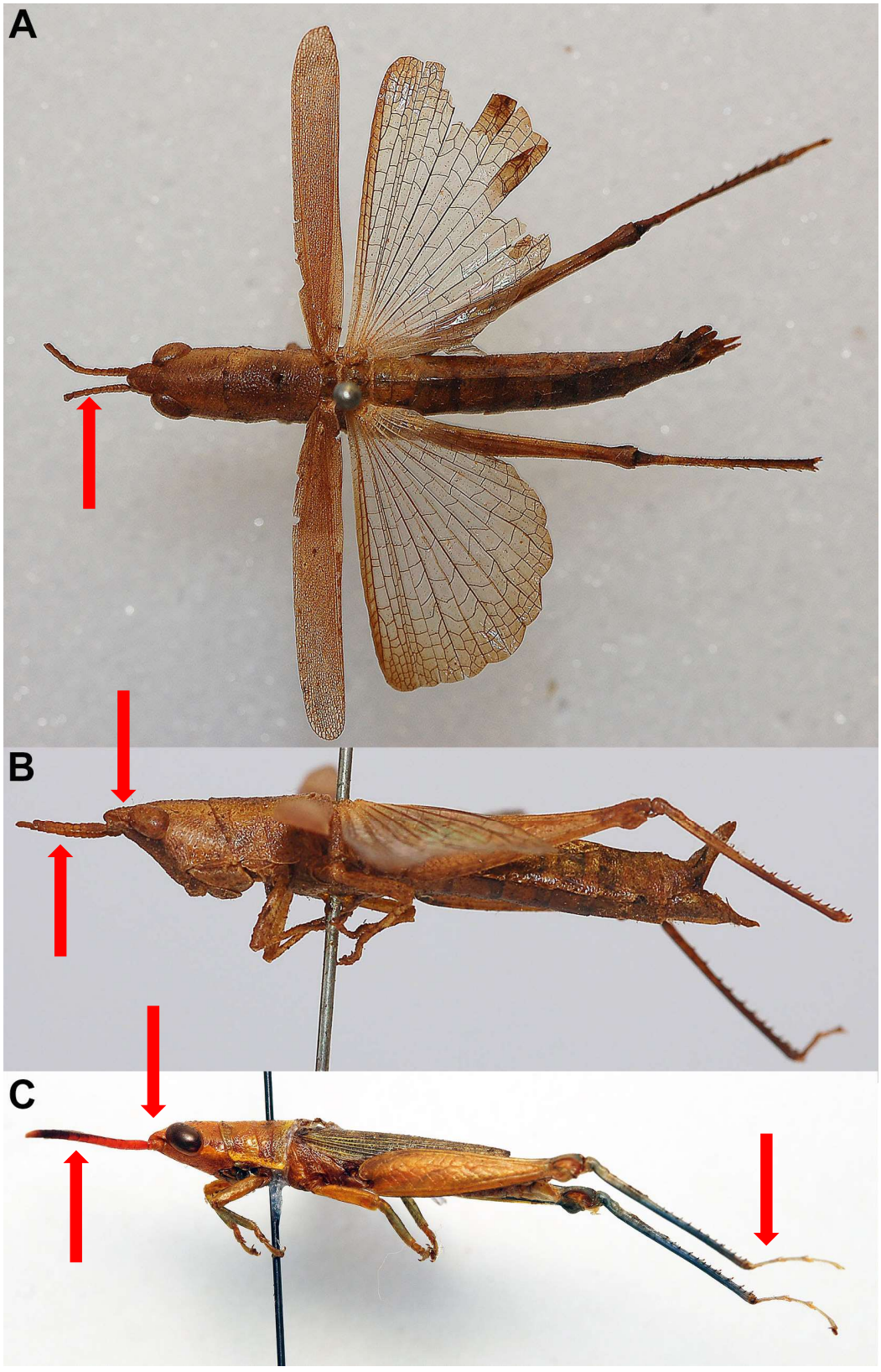

Figure 3.49. Papuasia and Pacific Islands Pyrgomorphidae 1. **A.** *Verdulia cycloidea* female dorsal view. **B.** *V. cycloidea* female lateral view. **C.** *Megra flava* male lateral view.

(*F. gracilis*)

5. Apterous. 6

5’. Tegmina and hind wings present (fig. 3.49C). (New Guinea Island) ……..***Megra**** **(2 spp.)**

(*M. flava, M. trimaculata*)

6. Segment 2 of hind tarsus subequal to or longer than metatarsus. 7

6’. Segment 2 of hind tarsus much shorter than metatarsus. 9

7. Head strongly depressed; head behind eyes distinctly wider than pronotum; male terminalia not elaborately specialized. 8

7’. Head not strongly depressed; head behind eyes not distinctly wider than pronotum; male terminalia very elaborated (fig. 3.50A,B). (New Guinea Island, Solomon Islands) .....***Modernacris**** **(6 spp.)**

(*M. callosa, M. carpentieri, M. controversa, M. forcipata, M. guentheri, M. simplex*)

8. Head much broader than its length, much wider behind eyes than pronotum; subgenital plate not elongate (fig. 3.50C,D). (New Guinea Island) .....***Paratarbaleus**** **(2 spp.)**

(*P. novaeguineae, P. spinosus*)

8’. Head not broader than its length, not so strongly narrowing toward pronotum; subgenital plate elongate (fig. 3.50E,F). (New Guinea Island, Bismarck Archipelago) .....***Noonacris**** **(2 spp.)**

(*N. novahibernica, N. pusilla*)

9. Fastigium of vertex short and broad; male terminalia not bulbous. 10

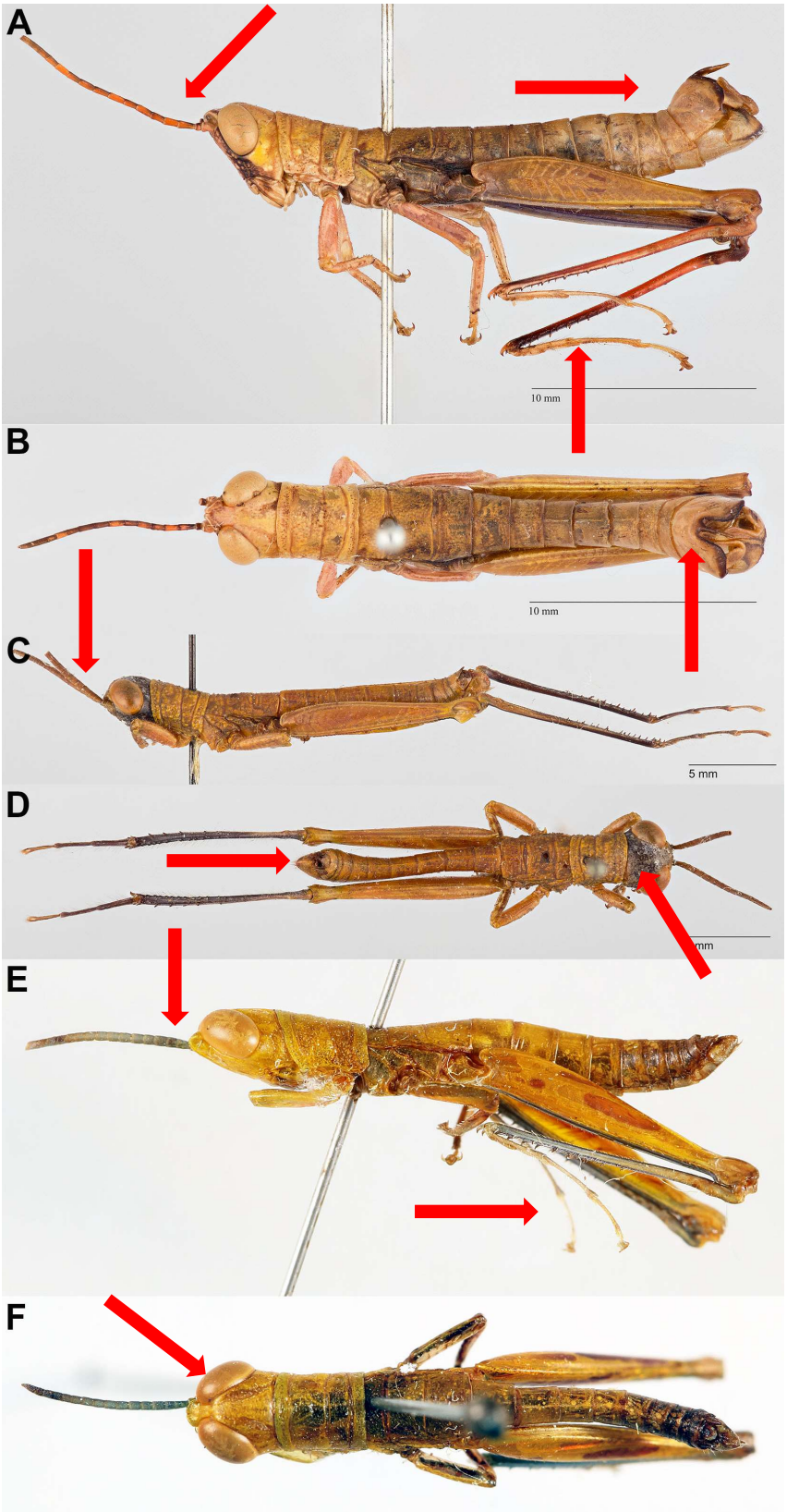

Figure 3.50. Papuasia and Pacific Islands Pyrgomorphidae 2. **A.** *Modernacris controversa* male lateral view. **B.** *M. controversa* male dorsal view. **C.** *Paratarbaleus novoguineae* male lateral view. **D.** *P. novoguineae* male dorsal view. **E.** *Noonacris pusilla* male lateral view. **F.** *N. pusilla* male dorsal view.

9’. Fastigium of vertex prominent; male terminalia enlarged and bulbous (fig. 3.51A,B). (New Caledonia) .....***Nerenia**** **(1 sp.)**

(*N. francoisi*)

10. Antennal segments all or almost all distinctly longer than their width; posterior margin of lateral pronotal lobe not or not strongly excised. 11

10’. Antennal segments subquadrate or but little longer than their width; posterior margin of lateral pronotal lobe strongly and roundly excised (fig. 3.51C,D). (New Guinea Island) .....***Buergersius**** **(1 sp.)**

(*B. olivaceus*)

11. Body not prominently tuberculate (except for meso-epistenal and sometimes a par of mid-dorsal lines of abdomen). 12

11’. Body beset with numerous prominent tubercles, especially on head and thorax; lower parts of thoracic meta-episterna (as well as of meso-episterna) with prominent tubercles visible from above (fig. 3.51E,F). (New Guinea Island) .....***Tarbaleopsis**** **(7 spp.)**

(*T. brunnea, T. hystrix, T. minor, T. proxima, T. stellae, T. tuberculata, T. willemsei*)

12. Head and fastigium of vertex narrower and head no wider than pronotum; eyes of males distinctly prominent (fig. 3.52A,B). (New Guinea Island) .....***Fusiacris**** **(2 spp.)**

(*F. spinata, F. uniformis*)

12’. Head and fastigum of vertex wide and head wider than pronotum; both sexes with eyes prominent (fig. 3.52C,D). (New Guinea) .....***Kapaoria**** **(3 spp.)**

(*K. flava, K. flavomaculata, K. novaeguineae*)

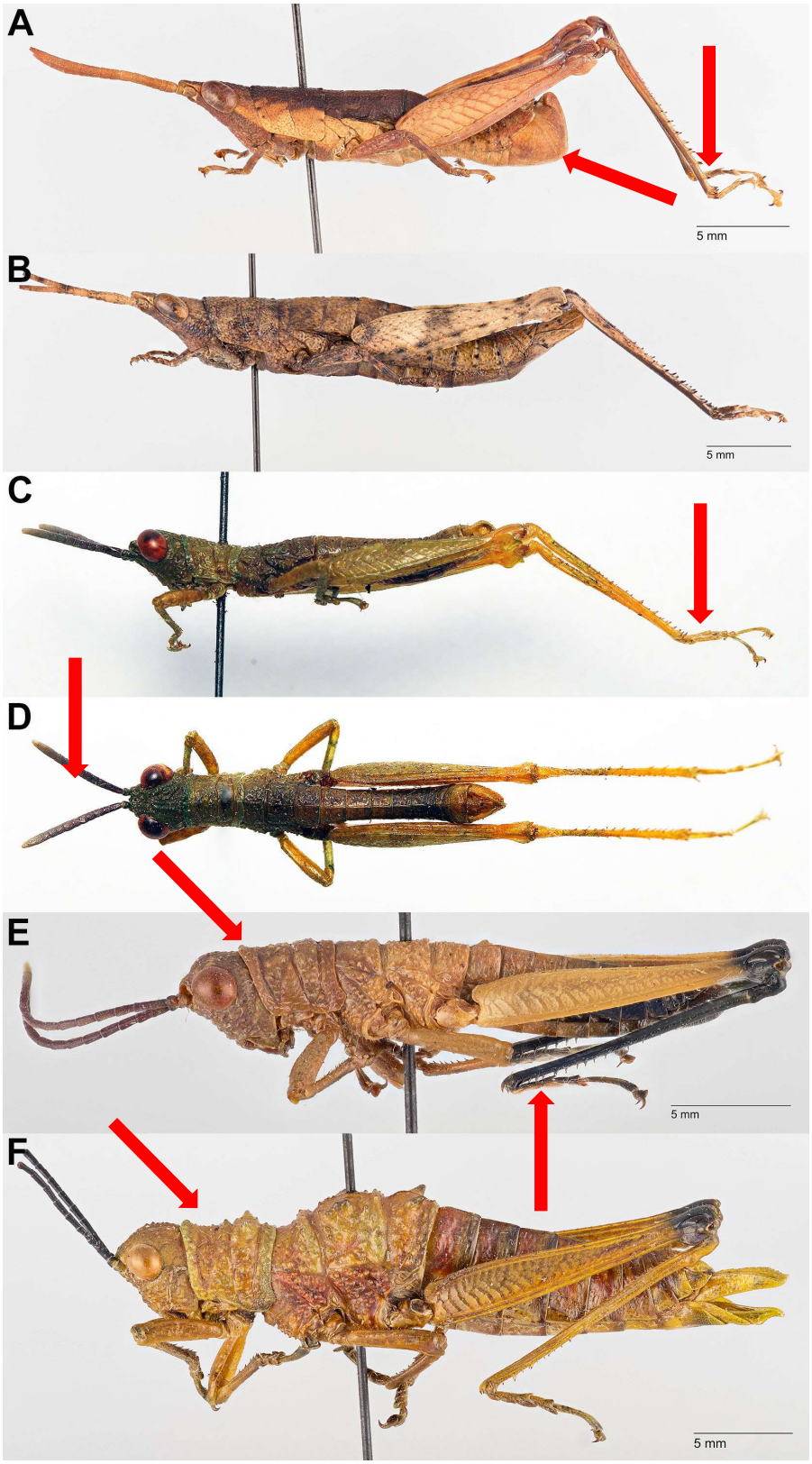

Figure 3.51. Papuasia and Pacific Islands Pyrgomorphidae 3. **A.** *Nerenia francoisi* male lateral view. **B.** *N. francoisi* female lateral view. **C.** *Buergersius olivaceus* male lateral view. **D.** *B. olivaceus* male dorsal view. **E.** *Tarbaleopsis hystrix* male lateral view. **F.** *T. hystrix* female lateral view.

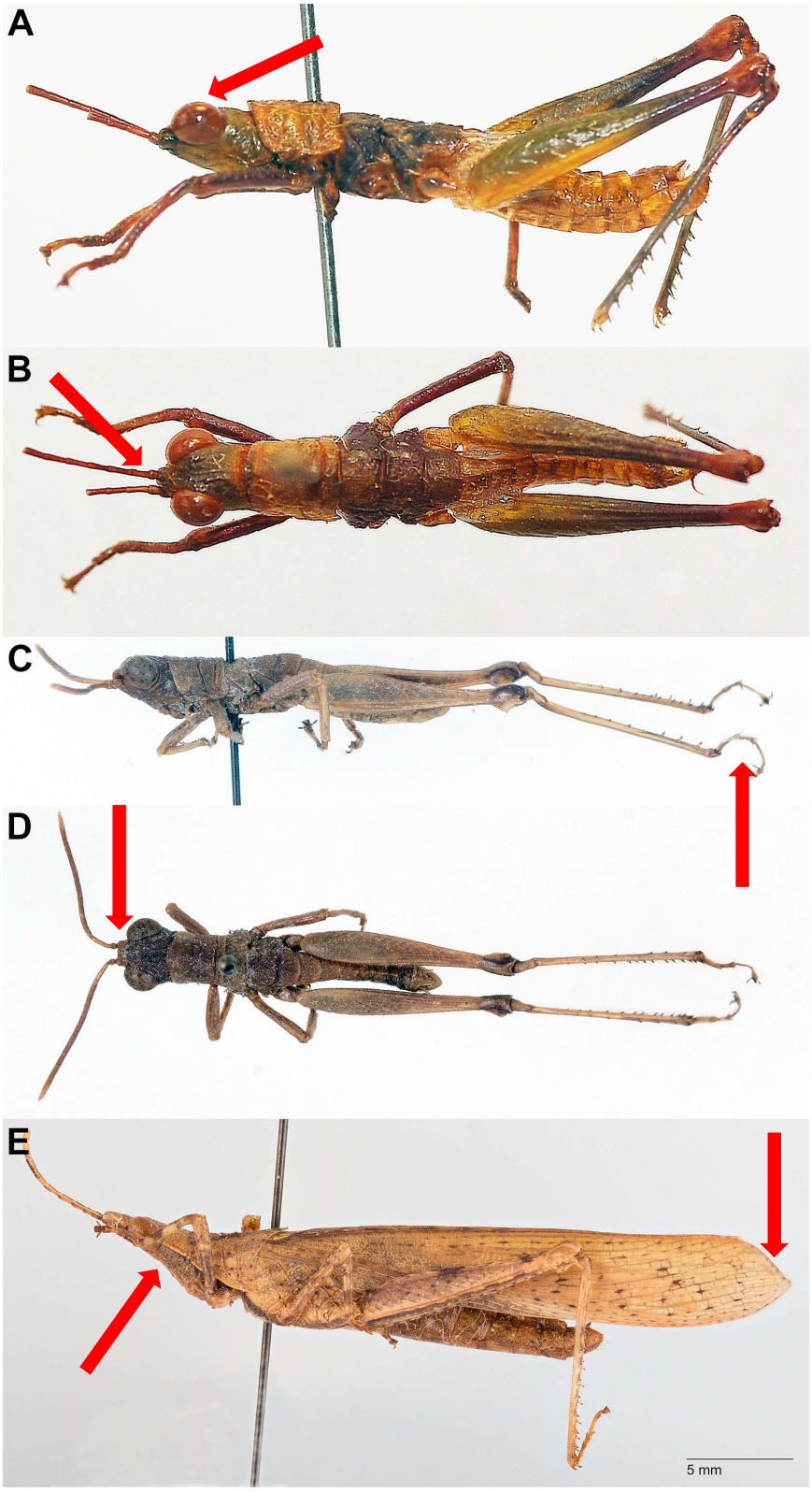

Figure 3.52. Papuasia and Pacific Islands Pyrgomorphidae 4. **A.** *Fusiacris spinata* male lateral view. **B.** *F. spinata* male dorsal view. **C.** *Kapaoria novoguineae* male lateral view. **D.** *K. novoguineae* male dorsal view. **E.** *Menesesia novaeguineae* male lateral view.

13. Tegmina with a distinct apical point about, or in advance of the middle of the apical margin; infero-posterior angle of lateral pronotal lobe distinctly acute or subacute. 14

13'. If tegmina and wings fully developed, tegmina with or without a distinct apical point. If distinct apical point present then, it is distinctly nearer the posterior margin rather than the anterior margin of the tegmina; infero-posterior angle of lateral pronotal lobe not distinctly acute, at most subacute. 15

14. Large body size (males at least 25 mm and females 35 mm); head very acute, frons very strongly oblique, subtending and angle of at most 25° with the vertex; tubercular ridge behind eye to inferior margin of pronotum strongly exaggerated, carina-like; infero-posterior angle of lateral pronotal lobe strongly acute (fig. 3.52E). (New Guinea Island) .....***Menesesia**** **(1 sp.)**

(*M. novaeguineae*)

14'. Small body size (males less than 25 mm and females less than 35 mm); head less acute, frons less oblique, subtending and angle of at least 30° with the vertex; tubercular ridge behind eye to inferior margin of pronotum less strong; infero-posterior angle of lateral pronotal lobe subacute (fig. 3.53A). (New Guinea Island) .....***Menesesiella**** **(2 spp.)**

(*M. occulta, M. weylandi*)

15. Frons very strongly concave, rugose with the pair of tubercles or callous spots on either side of and slightly below median ocellus very strongly developed; pronotum strongly rugose, usually with a prominent, angular, oblique ridge running forward and downward from the upper part of the lateral lobe to near the infero-anterior angle. 16

15'. Frons and pronotum not as above. 19

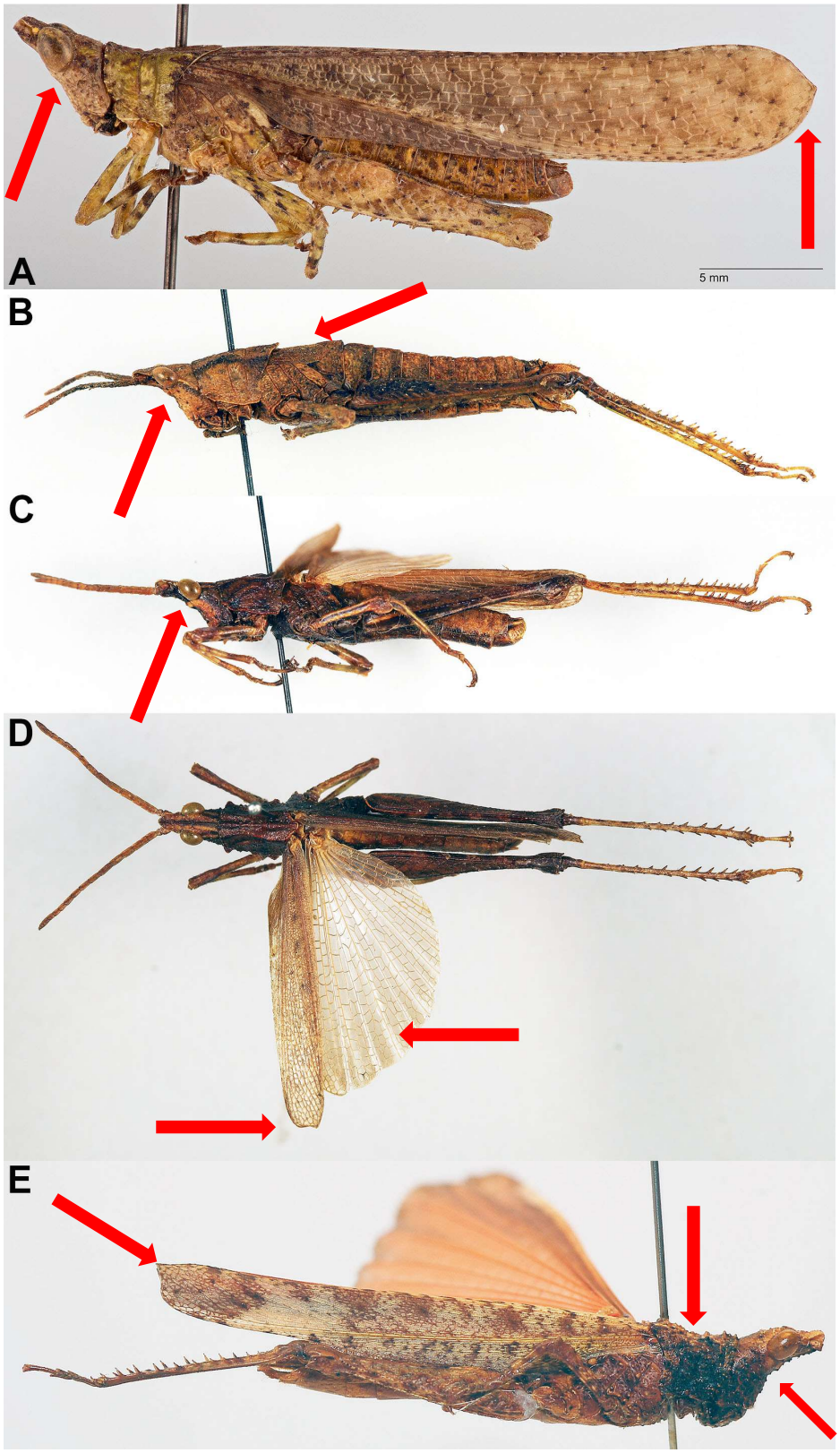

Figure 3.53. Papuasia and Pacific Islands Pyrgomorphidae 5. **A.** *Menesesiella occulta* male lateral view. **B.** *Stenoxyphellus brachypterus* female lateral view. **C.** *Stenoxyphula excisa* male lateral view. **D.** *S. excisa* male dorsal view. **E.** *Paradoriaella tuberculata* female lateral view.

16. Infero-posterior angle of pronotum strongly curved outwards; macropterous. 17

16’. Infero-posterior angle of pronotum not strongly curved outwards; tegmina and wings greatly reduced (fig. 3.53B). (New Guinea Island) .....***Stenoxyphellus*** **(1 sp.)**

(*S. brachypterus*)

17. Tegmina with apices produced or obliquely truncated, or, if transversely truncated (females), then at most sinuous or slightly emarginated, not distinctly excised; hind wings narrower with apex produced into a short point. 18

17’. Tegmina tapering, with apices abruptly and transversely truncated and distinctly excised (especially in females); hind wings broad with apices rounded (fig. 3.53C,D). (New Guinea Island) .....***Stenoxyphula****** **(2 sp.)**

(*S. excisa, S. microphallica*)

18. Tegmina strongly tapering from near the base (apices obliquely truncated and with a strong apical point); pronotum very rugose but the oblique ridge of the lateral lobe poorly developed and not forming a prominent point at the infero-anterior angle of the lobe (fig. 3.53E). (New Guinea Island) .....***Paradoriaella****** **(1 sp.)**

(*P. tuberculata*)

18’. Tegmina, if tapering, then not strongly so; pronotum with the oblique, callous ridge of the lateral lobe well developed and forming a prominent point at the infero-anterior angle of the lobe (fig. 3.54A). (New Guinea Island) .....***Stenoxyphus****** **(3 spp.)**

(*S. aurantiacus, S. expansus, S. variegatus*)

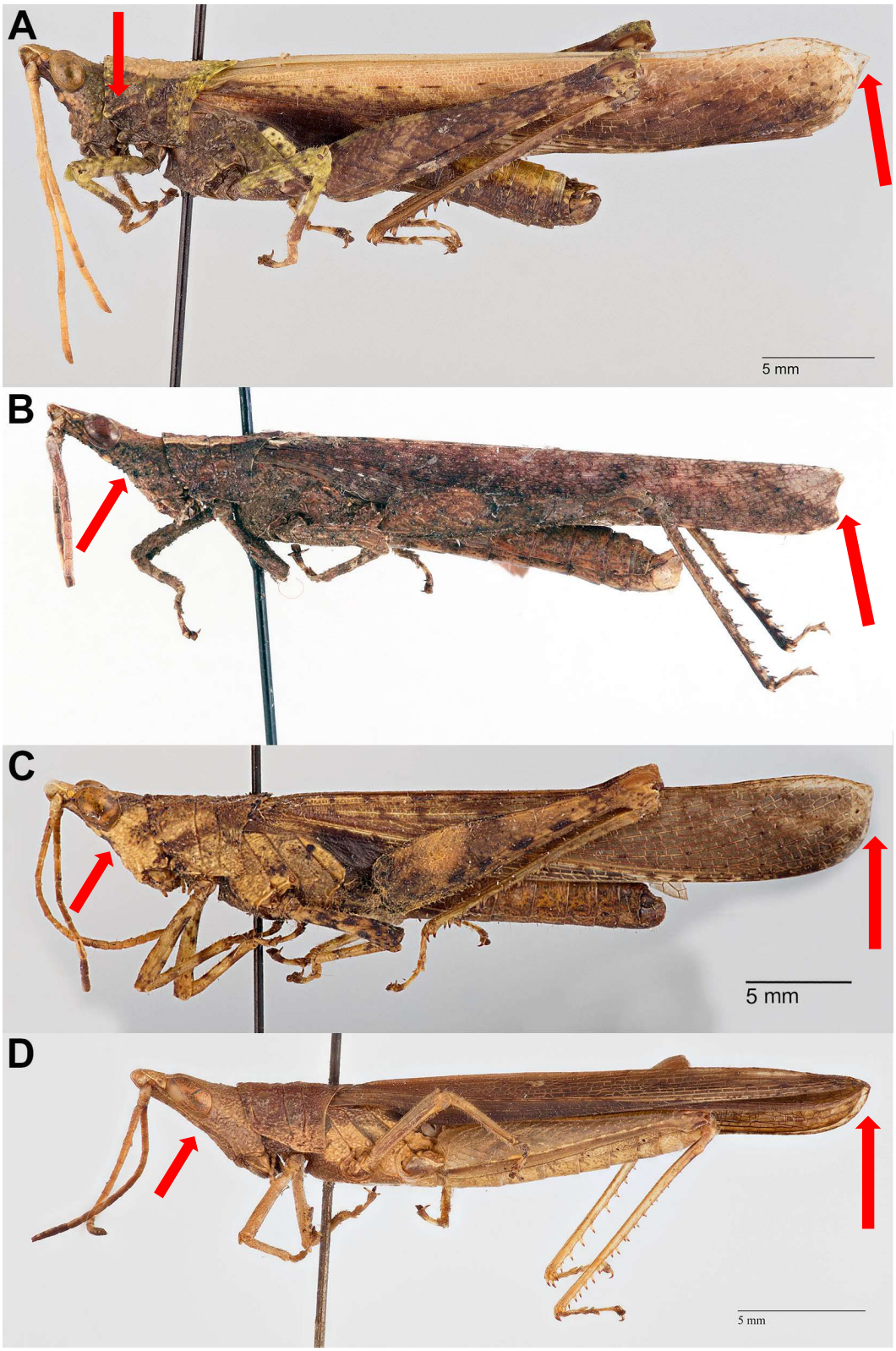

Figure 3.54. Papuasia and Pacific Islands Pyrgomorphidae 6. **A.** *Stenoxyphus aurantiacus* male lateral view. **B.** *Doriaella cinnabarina* male lateral view. **C.** *Desmoptera novoguineae* male lateral view. **D.** *Desmopterella angustata* male lateral view.

19. Tegmina with apices not strongly excised even if abruptly truncated and slightly emarginated; hind wings with apices rounded or bluntly pointed, not emarginated; ovipositor valves curved and hooked at apices; antennae not broadly expanded. 20

19'. Tegmina with apices abruptly truncated and normally strongly excised (especially in females); hind wings with apices angular and emarginated; ovipositor valves straight, serrated, but not hooked at apices; antennae sometimes broadly expanded (especially in females) (fig. 3.54B). (New Guinea Island) .....***Doriaella**** **(2 spp.)**

(*D. cheesmanae, D. cinnabarina*)

20. Tegmina not tapering from near the base, anterior margin usually curving rather abruptly into apical margin; large body size, more than 22 mm for males and 33 mm for females (fig. 3.54C). (New Guinea) .....***Desmoptera*** **(1 sp.)**

(*D. irianica*)

20'. Tegmina often tapering gradually from near the base, anterior margin curving more gradually into the apical margin; small body size, less than 22 mm for males and 35 for females (fig. 3.54D). New Guinea Island, Bismarck Archipelago)

……..***Desmopterella*** **(17 spp.)**

(*D. angustata, D. biroi, D. buergersi, D. cercata, D. circe, D. curvata, D. curvicercis, D. dahli, D. denticulata, D. esme, D. explicata, D. haani, D. marginata, D. prasina, D. sundaica, D. sylvatica, D. willemsei*)

3.2.12 Key to Pyrgomorphidae genera of Australia

Modified from Key (1972, 1984) and with information from Rentz et al. (2003).

Twelve genera, nine endemic to Australia.

1. Body extremely elongated with long subgenital plate. 2

1'. Not as above. 4

2. Micropterous. 3

2'. Apterous (fig. 3.55A,B). (East and Southeast Australia) .....***Psednura**** **(3 spp.)**

(*P. longicornis, P. musgravei, P. pedestris*)

3. Apex of male cerci bent (fig. 3.55C,D). (Southern Australia) .....***Psedna**** **(1 sp.)**

(*P. nana*)

3'.Apex of male cerci straight (fig. 3.55E,F). (Southern Australia)

.....***Propsednura**** **(2 spp.)**

(*P. eyrei, P. peninsularis*)

4. Body laterally compressed. 5

4'. Body not laterally compressed. 6

5. Tegmina not tapering from near the base, anterior margin usually curving rather abruptly into apical margin; large body size, more than 22 mm for males and 33 mm for females (fig. 3.54C). (Northeast Australia) .....***Desmoptera*** **(1 sp.)**

(*D. truncatipennis*)

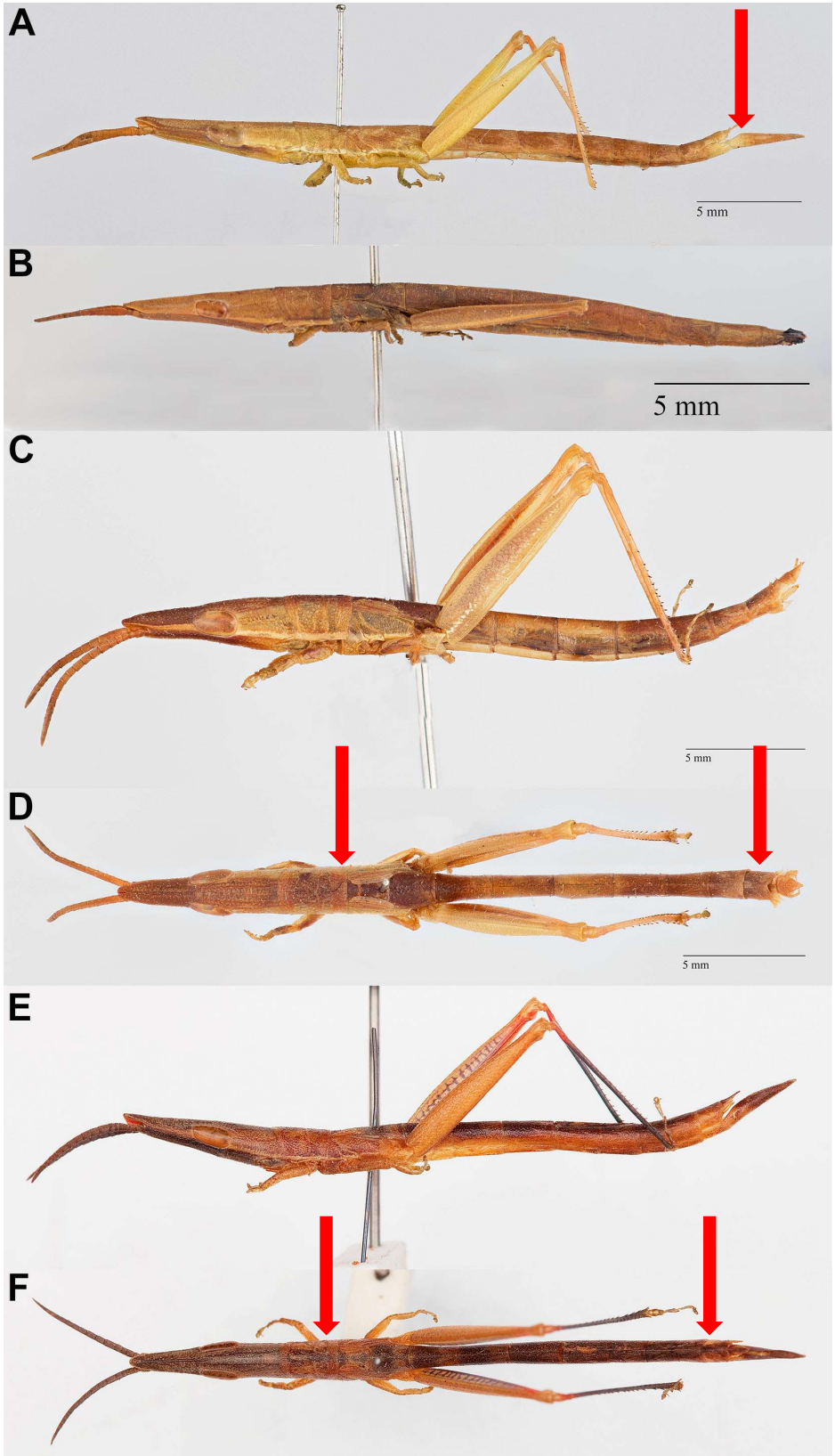

Figure 3.55. Australian Pyrgomorphidae 1. **A.** *Psednura musgravei* male lateral view. **B.** *P. musgravei* female lateral view. **C.** *Psedna nana* male lateral view. **D.** *P. nana* male dorsal view. **E.** *Propsednura peninsularis* male lateral view. **F.** *P. peninsularis* male dorsal view.

5’. Tegmina often tapering gradually from near the base, anterior margin curving more gradually into the apical margin; small body size, less than 22 mm for males and 35 for females (fig. 3.55D). (Northeast Australia.) .....***Desmopterella* (1 sp.)**

(*D. explicata*)

6. No row of tubercles running from eye to anterior lateral margin of pronotum. 7

6’. A row of tubercles running from eye to anterior lateral margin of pronotum. (North and East Australia) .....***Atractomorpha* (3 spp.)**

(*A. australis, A. hypoestes, A. similis*)

7. Tympanum present. 8

7’. Tympanum absent. 9

8. Posterior margin of pronotum unilobed (fig. 3.56C,D). (Southwestern Australia) .....***Scutillya** (1 sp.)**

(*S. verrucosa*)

8’ Posterior margin of pronotum bilobed (fig. 3.56A,B). (Central part of Northern Australia) .....***Petasida** (1 sp.)**

(*P. ephippigera*)

9. Cross veins on tegmina well developed, cells black. 10

9’. Cross veins weakly developed, cells not black (fig. 3.57A). (Southeast Australia) .....***Yeelana** (2 spp.)**

(*Y. argus, Y. pavonina*)

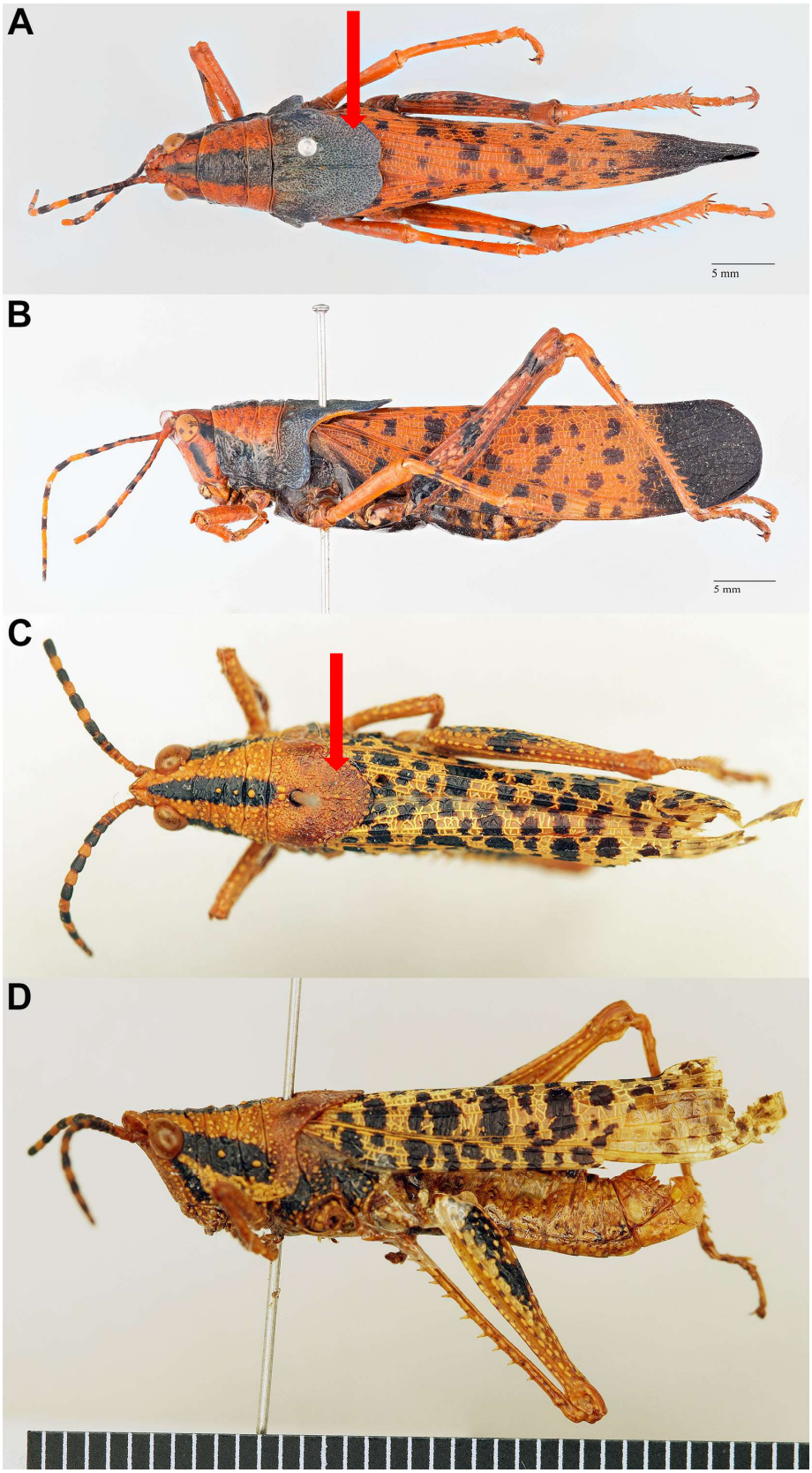

Figure 3.56. Australian Pyrgomorphidae 2. **A.** *Petasida ephippigera* male dorsal view. **B.** *P. ephippigera* male lateral view. **C.** *Scutillya verrucosa* male dorsal view. **D.** *S. verrucosa* male lateral view.

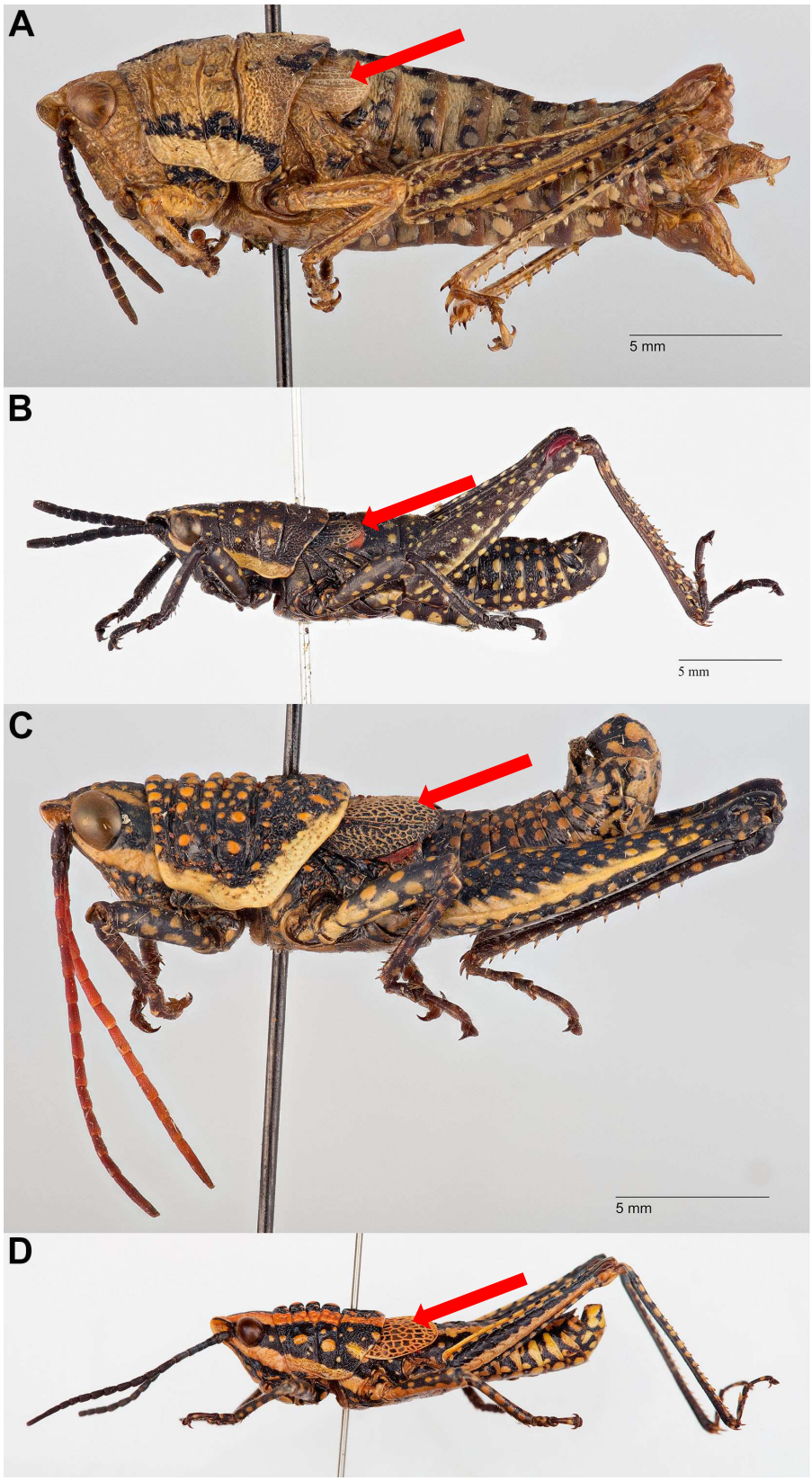

Figure 3.57. Australian Pyrgomorphidae 3. **A.** *Yeelanna argus* female lateral view. **B.** *Monistria concinna* male lateral view. **C.** *Greyacris picta* male lateral view. **D.** *Parastria reticulata* male lateral view.

10. Cells on tegmina numerous. 11

10’. Few cells, two or more fairly strong and direct longitudinal veins (fig. 3.57B).

(Throughout Australia except northern areas) .....***Monistria**** **(8 spp.)**

(*M. cicatricosa, M. concinna, M. consobrina, M. discrepans, M. latevittata, M. maculicornis, M. pustulifera, M. sulcata*)

11. Tegmina with small cells, non-granular (fig. 3.57C). (Central and Northern Australia)

.....***Greyacris**** **(2 spp.)**

(*G. picta, G. profundesulcata*)

11’. Tegmina with large cells, minutely granular (fig. 3.57D). (Central part of Northern Australia) .....***Parastria**** **(1 sp.)**

(*P. reticulata*)

3.2.13 Pyrgomorphidae genera of Europe (excluding Cyprus)

There are two species of Pyrgomorphidae from Europe. *Pyrgomorpha conica conica* (fig. 3.58A,B) with a distribution in the Mediterranean region and *Pyrgomorphula serbica* (fig. 3.58C,D), critically endangered, endemic to Mount Tara in Serbia (16 km^2) (Chobanov et al., 2016).

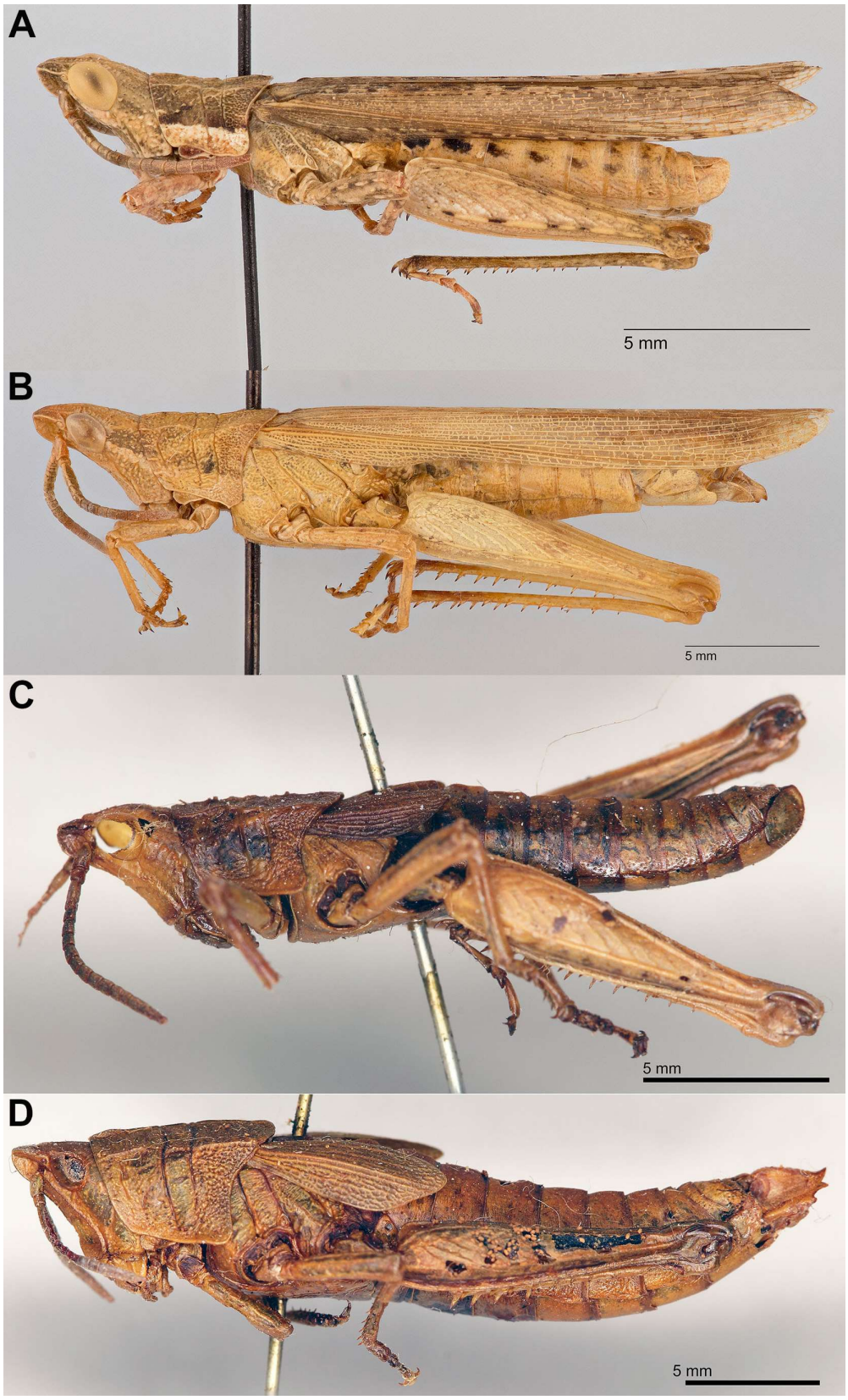

Figure 3.58. Europe Pyrgomorphidae. **A.** *Pyrgomorpha conica* male lateral view. **B.** *P. conica* female lateral view. **C.** *Pyrgomorphula serbica* male lateral view. **D.** *P. serbica* female lateral view.

CHAPTER IV

PHYLOGENY OF THE GRASSHOPPER FAMILY PYRGOMORPHIDAE (CAELIFERA, ORTHOPTERA) BASED ON MORPHOLOGY*

4.1 Abstract

The Pyrgomorphidae (Orthoptera: Caelifera) is considered one of the most colorful grasshopper families in the world (fig. 4.1), which contains about 500 species distributed worldwide. Commonly referred to as gaudy grasshoppers or bush grasshoppers, many pyrgomorphs are known to be aposematic and capable of sequestering plant secondary compounds. Several species are considered important agricultural pests, while some species are culturally important. Nevertheless, the phylogeny of this family has never been proposed based on a modern cladistics method. In this study, I present a phylogenetic analysis of Pyrgomorphidae, based on 119 morphological characters with 269 character states from 41 ingroup and 3 outgroup taxa, covering 28 out of 31 current recognized tribes. I recover the monophyly of the family and one of the two currently recognized subfamilies, Orthacridinae. The other subfamily, Pyrgomorphinae, is recovered as paraphyletic. Based on the most parsimonious tree, I propose four main clades and discuss about their defining morphological synapomorphies as well the biology and biogeography of the members of these clades. This is the first step toward building a natural classification for Pyrgomorphidae, which is an excellent model system for studying the evolution of interesting traits such as wing development, warning coloration and chemical defense.

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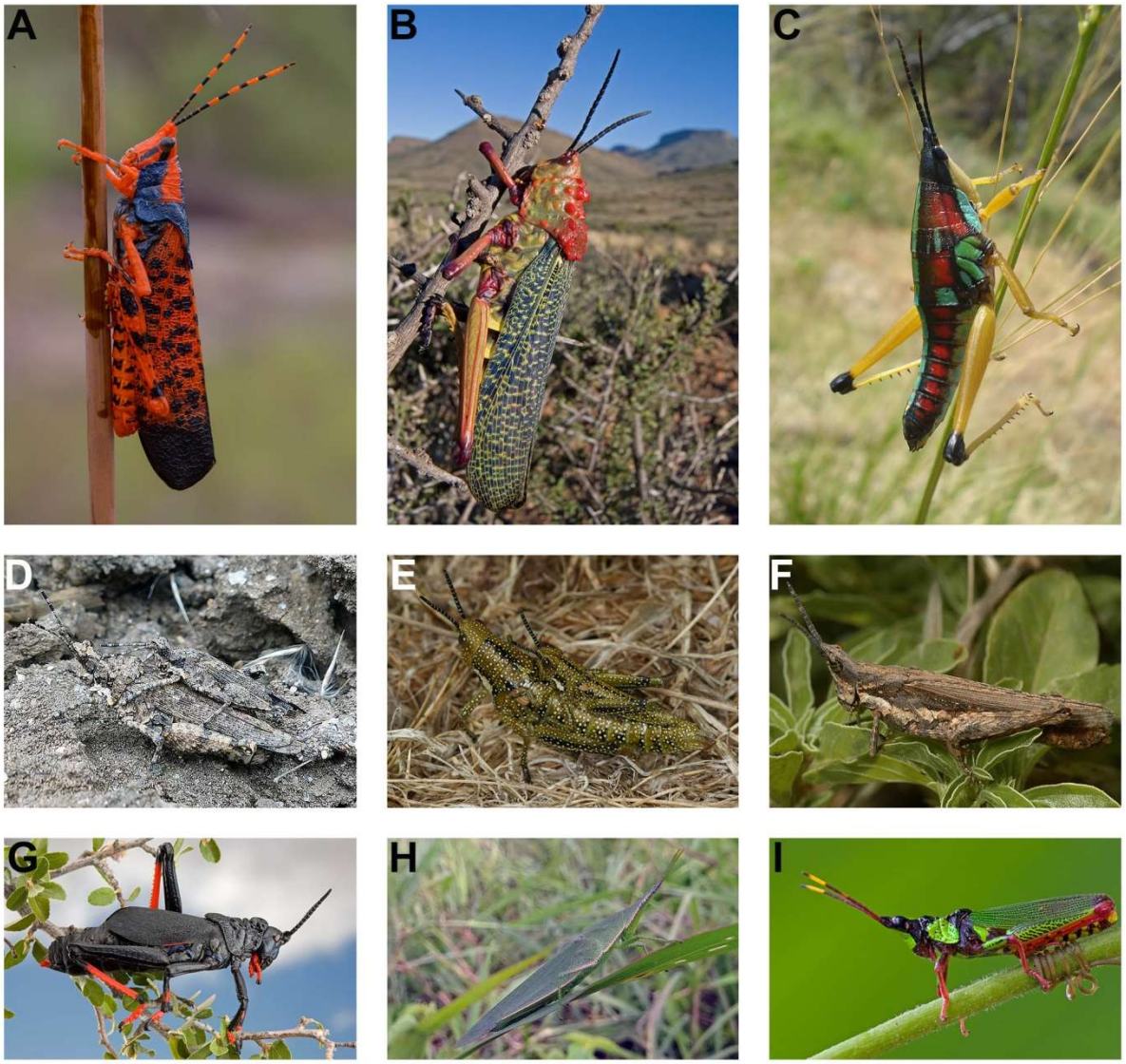

Figure 4.1. Alive Pyrgomorphidae. A. *Petasida ephippigera* (Australia); B. *Phymateus morbillosus* (South Africa); C. *Sphenarium histrio* (Mexico); D. *Chrotogonus hemipterus* (Mozambique); E. *Monistria* sp. (Australia); F. *Pyrgomorpha conica* (Greece); G. *Dictyophorus* sp. (South Africa); H. *Atractomorpha acutipennis* (Mozambique) and I. *Taphronota ferruginea* (Guinea). Photo credits: A. Nathan Litjens; B, G and I. Piotr Naskrecki; C and D. Ricardo Mariño-Pérez; E. Hojun Song; F. Roy Kleukers and H. Bert Foquet.

4.2 Introduction

Given the conspicuousness of many pyrgomorph species, their interesting biology, and cultural and economic importance, it is surprising that the taxonomy of the family as a whole has not been revised for the past 50 years, and that there is no phylogenetic hypothesis based on a modern cladistic analysis available. In this study, I present the first phylogenetic hypothesis of

Pyrgomorphidae based on 28 out of the 31 currently known tribes and a large number of external and internal morphological characters. Specifically, I aim to test the monophyly of the family and subfamilies, and to describe phylogenetic relationships among major clades within the family. I also provide extensive discussion about phylogenetically important morphological characters in light of the phylogenetic analysis. This study is intended to establish a strong foundation for future studies on the evolution of this fascinating family of grasshoppers.

4.3 Materials and methods

4.3.1 Taxon sampling

This study included 44 terminals (3 outgroups and 41 ingroup taxa). The ingroup taxa comprised 41 species from different genera representing 28 out of the 31 currently known tribes (90%) of Pyrgomorphidae (Table 4.1, figs 4.4-4.10). The remaining 3 tribes, Brunniellini (Philippines), Fijipyrgini (Fiji), and Malagasphenini (Madagascar), were not included because specimens from these tribes were not available at the time of the study. As for outgroup taxa, I included 3 species representing 3 families (Pamphagidae, Lentulidae, and Acrididae) of the superfamily Acridoidea. Because the purpose of this work was to study the internal relationships within Pyrgomorphidae, the outgroup taxa were represented by a single species from each family. The specimens used in this study were borrowed from the following institutions: Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (ANSP); The Natural History Museum, London, UK (BMNH); the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Although the specimens were already identified in several cases by well-known orthopterologists such as Decamps, Kevan, Hebard, and Key among others (Appendix B), the works of Dirsh (1963,

1965), Kevan (1976) and Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975) and Rentz et al. (2003) were used to confirm the identifications.

Table 4.1. List of species used in the present study. The classification is based on the information from the Orthoptera Species File.

Family	Subfamily	Tribe	Species
Pamphagidae			*Prionotropis h. hystrix* (Germar, 1817)
Lentulidae			*Lentula* sp.
Acrididae			*Guaranacris specularis* (Bruner, 1906)
Pyrgomorphidae	Orthacridinae	Chapmanacridini	*Chapmanacris sylvatica* Dirsh, 1959 (Ghana)
		Geloiini	*Pseudogeloius decorsei* (Bolívar, 1905) (Madagascar)
		Gymnohippini	*Gymnohippus marmoratus* Bruner, 1910 (Madagascar)
		Ichthiacridini	*Sphenacris crassicornis* Bolívar, 1884 (Mexico)
		Ichthyotettigini	*Ichthyotettix mexicanus* (Saussure, 1859) (Mexico)
		Mitricephalini	*Mitricephaloides rhodopterus* (Miller, 1934) (Malaysia)
		Nereniini	*Modernacris controversa* Willemse, 1931 (Solomon Islands)
		Orthacridini	*Acropyrgus cadeti* Descamps & Wintrebert, 1966 (Madagascar)
			Caprorhinus kevani Descamps & Wintrebert, 1966 (Madagascar)
			Orthacris incongruens Carl, 1916 (India)
		Popoviini	*Colemania sphenarioides* Bolívar, 1910 (India)
		Psednurini	*Psednura musgravei* Rehn, 1953 (Australia)
			Psedna nana (Rehn, 1953) (Australia)
		Sagittacridini	*Acanthopyrgus finoti* (Bolívar, 1905) (Madagascar)
		Verduliini	*Meubelia leytensis* Kevan, 1974 (Philippines)
	Pyrgomorphinae	Atractomorphini	*Atractomorpha aberrans* Karsch, 1888 (Congo)
		Chlorizeinini	*Chlorizeina unicolor* Brunner von Wattenwyl, 1893 (Thailand)
			Humpatella huambae Uvarov, 1953 (Angola)
		Chrotogonini	*Chrotogonus oxypterus* (Blanchard, 1836) (India)
			Tenuitarsus angustus (Blanchard, 1836) (Mauritania)
		Desmopterini	*Desmopterella angustata* Ramme, 1941 (Papua New Guinea)
		Dictyophorini	*Dictyophorus spumans* (Thunberg, 1787) (South Africa)
		Monistrini	*Monistria concinna* (Walker, 1871) (Australia)
		Omurini	*Omura congrua* Walker, 1870 (Peru)
		Petasidini	*Petasida ephippigera* White, 1845 (Australia)

Table 4.1. Continued

Family	Subfamily	Tribe	Species
		Phymateini	*Phymateus saxosus* Coquerel, 1861 (Madagascar)
			Zonocerus variegatus (Linnaeus, 1758) (Congo)
		Poekilocerini	*Poekilocerus pictus* (Fabricius, 1775) (India)
		Pseudomorphacridini	*Pseudomorphacris notata* (Brunner von Wattenwyl, 1893) (Myanmar)
		Pyrgomorphini	*Parasphena imatogensis* Rehn, 1942 (Sudan)
			Pyrgomorpha vignaudi (Guérin-Méneville, 1847) (Central African Republic)
			Anarchita aptera (Bolívar, 1904) (India)
			Zarytes squalinus (Saussure, 1884) (India)
		Schulthessiini	*Schulthessia biplagiata* Bolívar, 1905 (Madagascar)
		Sphenariini	*Mekongiella kingdoni* (Uvarov, 1937) (China)
			Rubellia nigrosignata Stål, 1875 (Madagascar)
			Sphenarium histrio Gerstaecker, 1884 (Mexico)
			Prosphena scudderi Bolívar, 1884 (El Salvador)
		Tagastini	*Tagasta indica* Bolívar, 1905 (India)
		Taphronotini	*Aularches miliaris* (Linnaeus, 1758) (Thailand)
			Taphoronota ferruginea (Fabricius, 1781) (Cameroon)

4.3.2 Classification

The classification used in this work followed the current systematic arrangement adopted by the Orthoptera Species File (Cigliano et al., 2018). Primarily this classification follows the groups "A" and "B" and the tribes recognized by Kevan (1976) and Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975). Their general characteristics are presented in table 4.2.

Table 4.2. General characteristics of groups A and B of Kevan et al. (1969a, b, c, d; 1972).

Group A	Group B
Metasternal pits usually large, connected by one suture	Metasternal pits usually small, joined by two sutures
Body form generally cylindrical or elongated	Body form usually but not always distinctly fusiform, or heavy or robust, or both
Hind femora often having both basal lobes subequally produced or the dorsal more prominent	Hind femora always with ventral basal lobe more prominent
Fastigium of vertex often (but by no means usually) short and blunt)	Pronotum sometimes with large tubercles
Predominantly 'Gondwanian'; absent form Palaeartic and South American regions but occurring in Mexico; poorly represented in Africa (except Madagascar)	Predominantly circumtropical and subtropical (poorly represented in the Americas), some extending to Palaeartic region; very strongly represented on Africa but few species in Madagascar; Australian Pyrgomorphidae belong mostly to this group

4.3.3 Character sampling

I consulted Dirsh (1963, 1965), Kevan et al. (1969, 1970, 1971, 1972, 1974), and Rentz et al. (2003) in order to obtain characters that had been traditionally used in the pyrgomorph taxonomy. Additionally, I conducted a comprehensive study of both external and internal morphology in search of additional characters. I followed Dirsh (1965) and Rentz et al. (2003) for external morphology terminology and Kevan (1976), Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975), and Eades (2000) for genitalia (epiphallus, ectophallus, and endophallus) terminology. The complete list and description of the 119 morphological characters (Figs 4.4-4.18) are presented in the Results section. The matrix is presented in Table 4.3.

4.3.4 Dissection methods

Dried museums specimens were relaxed by soaking their posterior portion of abdomen under boiling water for a few minutes until they were soft enough to extract internal genitalia. This was done by inserting a tip of forceps under the phallic structure and by gently pulling it. Dissected phallic structures were placed in 10% KOH solution for 30-120 min to dissolve muscle tissues. Dissolved muscles were removed in 70% ethanol and the entire structure was rinsed thoroughly. The epiphallus was separated from the ecto-endophallus complex. Both pieces were placed in genital vials with glycerin. This dissection procedure was based on Hubbell (1960).

4.3.5 Digital imaging and illustration

All of the specimens used in this study were photographed in lateral and dorsal views. Also the internal genitalia were photographed in two parts; the epiphallus and the ecto/endophallus. Other specific close-up photographs were taken to illustrate certain characters and their states. The

images of all preserved specimens and their associated genitalia were taken using the Visionary Digital BK Plus Imaging System in combination with a Canon EOS 7D camera using 65 and 100 mm lenses to take multiple images at different depths of field. After this, Adobe Lightroom 3 (v.3.2) was used to import the photos and transform them from RAW files to TIFF's and then Zerene Stacker (v.1.02) was employed to stack the image slices into a single focused image. Finally, Adobe Photoshop CS5 Extended was utilized, when necessary, to adjust light levels, background coloration, sharpness, and to add an accurate scale bar. Additionally, line drawings were made for important diagnostic characters using a camera lucida attached to Leica M205C. The illustrations were scanned and digitized using the Wacom Cintiq Tablet in Adobe Photoshop. Final composition of the plates was made in Adobe Photoshop.

4.3.6 Cladistic analysis

A data matrix consisting of 44 terminal taxa (41 ingroup and 3 outgroups) and 119 morphological characters with 269 character states was compiled in WinClada (Nixon, 2002). Non-applicable data were recorded as "-" and missing data as "?". 30 characters were neomorphic and 89 transformational (Sereno, 2007). For the uninformative states I atomize the characters using contingent coding (Brazeau, 2011). All the characters were coded non-additively and equally weighted. The data matrix used in this analysis is presented in Table 4.3. I searched for the most parsimonious trees in NONA (Goloboff, 1995) using the commands "rs 0", "hold 10000", "mult*1000", "max*", and "best". WinClada (Nixon, 2002) was used to view the trees and to calculate a strict consensus tree. The same data matrix was submitted to TNT (Goloboff et al., 2003) for an independent analysis using a combination of sectorial search,

drifting, tree fusing (Goloboff, 1999), and ratchet (Nixon, 1999). Bremer support values (Bremer, 1994) were calculated by holding suboptimal trees ten steps longer in TNT.

Table 4.3. Character matrix used in this analysis

Taxa	0 0123456789	1 0123456789	2 0123456789	3 0123456789	4 0123456789	5 0123456789	6 0123456789
Prionotropis	0000020-00	-010101001	0001----11	111-102111	1021011022	2000001202	02-0221000
Lentula	0200020-00	-010101001	0011----00	-11-0-1100	1000011001	0001121001	00-0001100
Guaranacris	1100000100	-0100-0-01	0011-0-110	-11-111101	1001011101	0002120101	00-0111000
Chapmanacris	2210002000	0010101001	101000-011	10-00-0100	0000000001	0000110000	00-0001100
Pseudogeloius	2200102110	2010101001	1011010111	00-10-0101	0000000002	2000101000	02-0001100
Gymnohippus	2101020010	2011111101	0010010100	-1110-0100	0000110021	2001011000	01-0011100
Sphenacris	2101100100	2011111101	001100-111	11110-0101	0000010122	2000111001	00-0221100
Mitricephaloides	2200000000	2010101001	101100-100	-1010-1100	0001010001	0000110001	00-0001100
Modernacris	2200010000	20110-0-01	001100-000	-1110-0110	0000000001	0001120001	00-0001110
Acropyrgus	2101111000	0011110-01	001100-110	-1110-0110	0000020101	0002021000	00-0111100
Caprorhinus	2111102100	2010101011	0011010111	11112-0110	0000000001	0000111001	00-0111100
Orthacris	2201010000	200-0-0-01	0011010111	10-10-0100	0000000001	0001110000	00-0001100
Colemania	2210002200	200-101001	000100-111	11012-0100	0000000000	0000110101	00-0001100
Acanthopyrgus	2210002010	2010101001	001100-111	11010-0100	0000010101	0011121001	00-0011100
Meubelia	2200010000	2010101000	-01100-011	10-00-0100	0000011101	0002120001	00-0001100
Atractomorpha	2010000100	2011111011	101100-111	1111101101	1001011102	0002121100	00-0111000
Chlorizeina	2110010000	2010101001	0001010111	1111101111	1000011000	0000111101	00-0111100
Humpatella	2201010000	2011101001	1001010111	1111101100	0001001000	0002111101	00-0111100
Chrotogonus	2100010001	2011111101	1001011111	1111121111	0111111122	2002011101	00-0010100
Tenuitarsus	2100011001	2010101101	1001011111	1111121111	0111101122	2002021001	00-0000001
Desmopterella	2210001000	2010101001	0011010111	1111101101	0010021201	0000111000	00-0111100
Dictyophorus	2001120100	210-0-0-01	100110-111	10-1111110	0021021230	3002101111	1-10111000
Ichthyotettix	2200011000	2011111011	0011011111	11110-0101	0001010020	2000101001	00-0111100
Monistria	2011110000	2010101001	0001010111	1111131101	0000021200	0002101011	1-00111000
Omura	2010002300	2010101001	001000-111	10-12-0111	1001021202	0001101100	00-0111000
Petasida	2201020100	200-0-0-01	1001110111	11111120-1	0021121201	0001101111	1-00110000
Phymateus	2201020100	200-0-0-01	1101110111	1111111101	0011011010	1001101111	1-00111000
Zonocerus	2201020000	200-0-0-01	110110-111	1111111101	0001001000	0001101111	1-00001000
Poekilocerus	2201010000	2010101001	1001110111	1111111101	0011011001	0000101111	1-00111000
Psedna	2010102100	2010101001	1011010111	10-00-0101	00000-1?00	0100101001	00-1001000
Psednura	2010102100	2010101001	1011010111	10-00-0101	00000-1?00	0100101001	00-1001000
Pseudomorphacris	2100001000	000-101011	1011010111	10-1101111	0001021101	0001101100	00-0111000
Anarchita	2100102000	2010101011	0011011110	-110100111	1000001001	0000001101	00-0110000
Parasphena	2101111000	200-101011	0001011111	1111101111	1001111101	0001101101	00-0111000
Pyrgomorpha	2100000100	2010101011	1001011111	1111101101	1001011101	0001101100	00-0110000
Zarytes	2000102000	2010101011	0011011111	1111100111	1001011101	0001101101	00-0110000
Schulthessia	2110002000	0010101011	0011010111	1111101111	1001121202	0002121100	00-0111020
Mekongiella	2201020000	2010101001	1001010111	1111131101	1001011101	0002101101	00-0111000
Prosphena	2001000200	1010101011	0001010111	1111131101	1001020201	0001101101	00-0111000
Rubellia	2201000100	2010101001	0001010111	1111131101	1001011100	0002101101	00-0111000
Sphenarium	2201001100	1010101001	0011010111	1111131101	1001020100	0002101101	00-0111000
Tagasta	2210000000	0010101011	0001010111	1111101101	1001011101	0002121100	00-0111000
Aularches	2201020000	200-0-0-00	-00110-111	10-11110-1	0011011110	3000101111	1-00011000
Taphronota	2101000000	200-100-01	100110-111	10-0111101	0011011120	0000101111	1-00111000

Table 4.3. Continued

Taxa	7 0123456789	8 0123456789	9 0123456789	10 0123456789	11 012345678
Prionotropis	11--000100	0010000010	000011-000	0000000111	0--110011
Lentula	0---------	--0-000010	0000110000	0000000111	0--100011
Guaranacris	11--000001	0011000010	0100110?00	0000001111	0--110011
Chapmanacris	0---------	--0-111000	0000001000	0000011110	012101000
Pseudogeloius	0---------	--0-101301	0000001000	0000011111	111101000
Gymnohippus	0---------	--0-001101	0000001000	1000011200	10-100000
Sphenacris	0---------	--0-000211	0000001000	0000011111	012100100
Mitricephaloides	11--0-----	--11101001	1000001000	0000011111	012101000
Modernacris	0---------	--0-101001	1000001000	0000011011	010200000
Acropyrgus	0---------	--0-000211	0000001000	0000011111	112100000
Caprorhinus	1001------	--0-001100	0000001000	0000011111	112100000
Orthacris	0---------	--0-000111	0000001000	0000011111	112100000
Colemania	1020------	--0-000101	0011001000	1000011111	112100100
Acanthopyrgus	0---------	--0-000101	0000001000	1000011101	112100100
Meubelia	1011------	--0-001200	0000001000	1000011110	010000100
Atractomorpha	11--001001	0011000111	0000001000	0010011111	012100000
Chlorizeina	11--001001	0011001121	0000001010	0000011111	012100000
Humpatella	1010------	--0-001121	0000001010	0000011111	112100000
Chrotogonus	11--001001	1010000201	0000001101	0000011111	012100000
Tenuitarsus	11--001001	1010001201	0000001101	0000011111	012100000
Desmopterella	11--000001	0010000101	0000001000	0000011111	012100100
Dictyophorus	11--000110	0011000200	0001001000	0000011111	012100000
Ichthyotettix	0---------	--0-1010?1	0000001000	0001011111	012000000
Monistria	11--100100	0011000200	0001001000	0000010111	011100100
Omura	0---------	--0-000110	0000001000	0000011111	012100000
Petasida	11--000110	0011000200	0001001000	0000011111	011100100
Phymateus	11--000101	0011000100	0011001000	0100011111	012100000
Zonocerus	11--000101	0111000100	0011001000	0000011111	011100100
Poekilocerus	11--000101	0011000100	0011001000	0100011111	012100100
Psedna	1010------	--0-001011	0100001000	0000010111	011100000
Psednura	0---------	--0-001011	0100001000	0000010111	110100000
Pseudomorphacris	11--011001	0010001111	0000001000	0000111111	011101000
Anarchita	0---------	--0-000111	0000001101	0000011110	012100000
Parasphena	0---------	--0-000111	0000001101	0000011111	012100000
Pyrgomorpha	11--001001	0010000110	0000001101	0000011110	012100000
Zarytes	11--001001	--10000111	0000001101	0000011110	012100000
Schulthessia	11--001001	0010000110	0000001101	0000011110	012100000
Mekongiella	0---------	--0-000210	0000001001	0000011111	012100100
Prosphena	1020------	--0-000210	0000001001	0000011111	012100100
Rubellia	11--100101	0011000211	0000001001	0000011111	012100000
Sphenarium	1020------	--0-000211	0000001001	0000011110	012100100
Tagasta	11--011001	0011000110	0000001010	0000011110	012100000
Aularches	11--000110	0011000100	0001001100	0000011111	012100000
Taphronota	11--000100	0011000100	0001001?00	0000011111	112100100

4. 4 Results

4.4.1 Phylogenetic analysis

The analysis resulted in 8 most parsimonious trees of 541 steps with the consistency index (CI) of 0.28 and retention index (RI) of 0.55. One of the most parsimonious trees is shown as a preferred tree in fig. 4.2. The strict consensus of these trees collapsed 7 nodes (L = 560, CI = 0.27, RI = 0.52). Bremer support values are shown in the consensus tree together with the number of synapomorphies per node (fig 4.3).

I recovered the family Pyrgomorphidae as a monophyletic group, which is supported by 8 synapomorphies. Of these, one is the presence of a groove in the fastigium and the others are the characters from the internal genitalia. Concerning the two subfamilies, Orthacridinae was recovered as monophyletic, while Pyrgomorphinae was recovered as paraphyletic. Overall, this analysis found that Pyrgomorphidae consisted of four major clades, which I tentatively refer to as clades A, B, C, and D. Because the majority of the tribes included in this analysis were represented by only a single species, I was unable to test the monophyly of these tribes. However, I included multiple taxa for some of the tribes, for which I could test the tribe-level monophyly. I found Chrotogonini (2), Sphenariini (4), Phymateini (2), and Psednurini (2) to be monophyletic. Particularly, I found overwhelming support (<9) and numerous synapomorphies for Chrotogonini (16) and Psednurini (10). I recovered Pyrgomorphini (4), Orthacridini (3), and Taphronotini (2) as paraphyletic. Of these, all included members of Pyrgomorphini (105 spp. in 29 genera), which is the most species-rich tribe within the family, were found in the clade D. Orthacridini (58 spp. in 11 genera) is the second most species-rich tribe and all its members were recovered as part of the clade A.

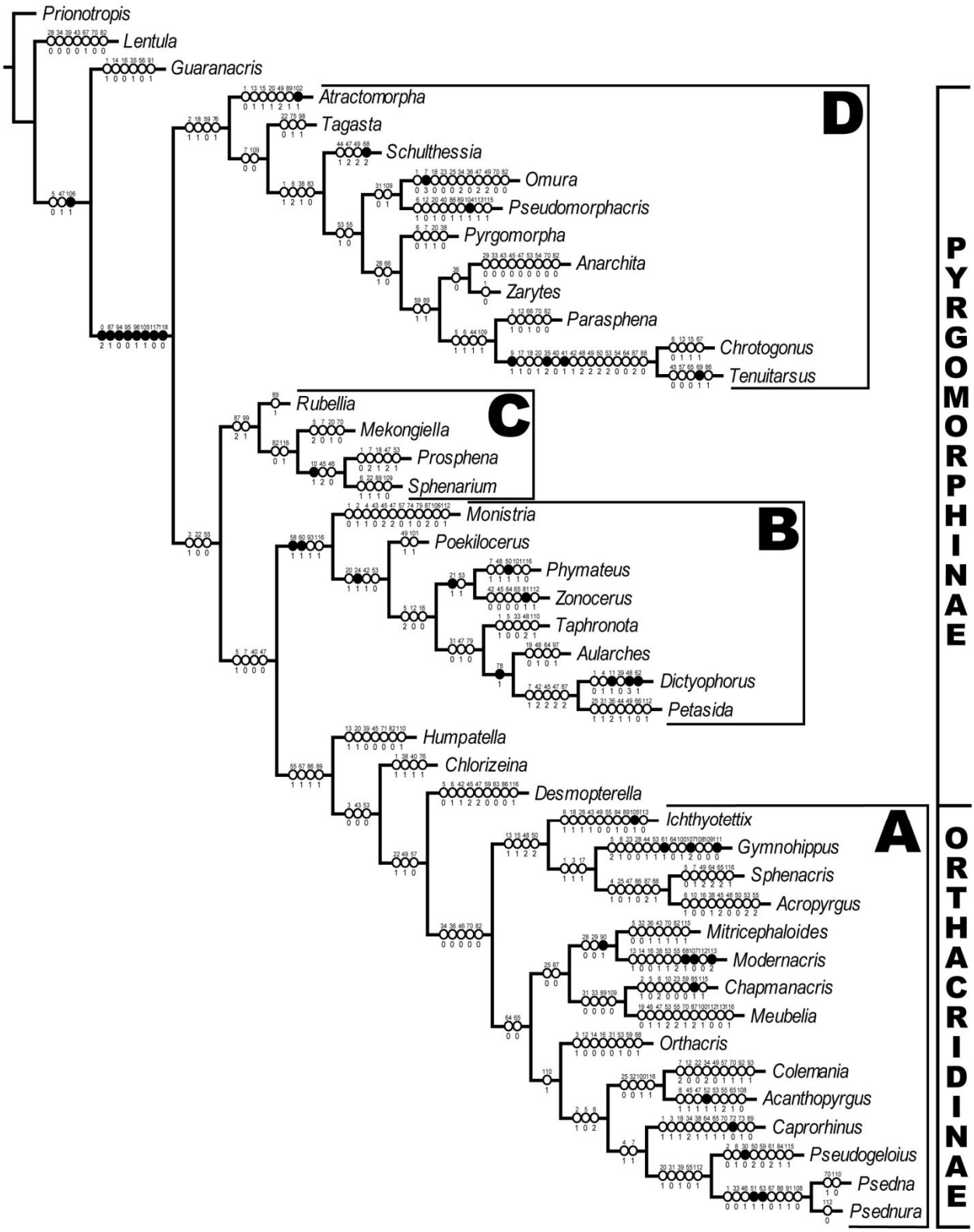

Figure 4.2. One of the 8 most parsimonious trees. Length 541 steps with consistency index (CI) of 0.28 and retention index (RI) of 0.55.

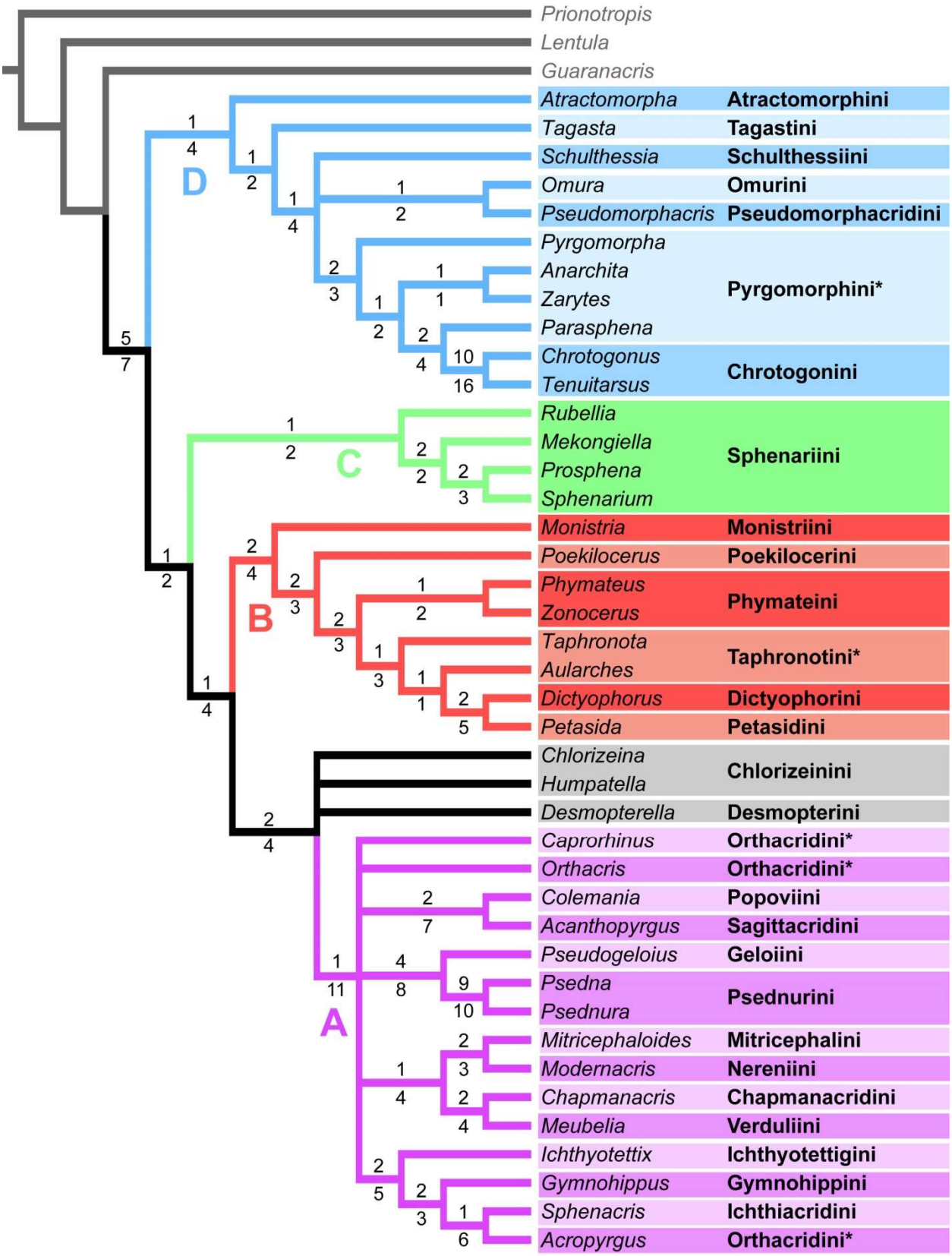

Figure 4.3. Strict consensus tree. 7 nodes collapsed (L = 560, CI = 0.27, RI = 0.52). Bremer support is the upper value and number of synapomorphies is the lower value at each node.

4.4.2 Description of characters, including comments on character optimizations

Because this study represents the most comprehensive morphological phylogeny of Pyrgomorphidae to date, I feel compelled to provide detailed descriptions and commentaries on the morphological characters used in the analysis. I optimized the characters on the preferred phylogeny (fig. 4.2). Unless specifically mentioned as the DELTRAN or ACCTRAN optimization, most characters were unambiguously optimized. CI and RI values are shown for each character, and those characters without these values (e.g. due to being autapomorphic) are characterized as uninformative (UNINF). After each characteristic, I used character and state number between parentheses.

4.4.2.1 Head

The most conspicuous and defining characteristic in Pyrgomorphidae is the groove in the fastigium in the head (0:2). In general, the groove runs throughout all the fastigium (10:2). The members of the clade B are characterized by very deep groove (24:1) as well as a smooth texture on the surface of the head (12:0, 14:0 & 16:0). Generally, the members of the clade D have a row of tubercles behind the eye (18:1). Eyes are in general oval in the clade A (22:1) and circular in the clades B and C (22:0).

0. Fastigium: (0) absent, (1) present without groove, (2) present with groove (fig. 4.18H). CI= 1.0, RI = 1.0. I followed the definition of Snodgrass (1993), Key (1979), and Torre-Bueno (1989) who defined the fastigium as an anterior projection of vertex. Kevan and Akbar (1964) discussed that one of the defining characteristics that distinguish members of

Pyrgomorphidae from other groups is the presence of a groove in the fastigium, which is an uncontroverted synapomorphy of Pyrgomorphidae.

1. Antennae, length compared to combined length of head and pronotum: (0) shorter (fig. 4.6D), (1) as long as (fig. 4.4C), (2) longer (fig. 4.6C). CI = 0.14, RI = 0.42. The antennae in the majority of Pyrgomorphidae are longer or as long as the head and pronotum together with independent reductions in size across the Pyrgomorphidae. The shorter antennae are a synapomorphy for the highly specialized *Psedna* and *Psednura* (Psednurini).
2. Antennal base, position relative to lateral ocelli in lateral view: (0) below and behind (fig. 4.17J), (1) in front of (fig. 4.4B). CI = 0.11, RI = 0.33. Most Pyrgomorphidae have the antennal base below and behind the lateral ocelli.
3. Antennae, antennomere junctions: (0) continuous (fig. 4.5A), (1) non-continuous (fig. 4.17J). CI = 0.16, RI = 0.72. The antennae with non-continuous antennomere junctions are present in the clades B and C. The clade A has the antennomere junctions continuous with three independent transformation to non-continuous junctions (*Orthacris*, *Caprorhinus* and the clade consisted of *Gymnohippus*, *Sphenacris* and *Acropyrgus*). All members of clade D possess continuous antennomere junctions except for the genus *Parasphena*.
4. Antennae, antennomere form: (0) rectangular (fig. 4.17J), (1) quadrate (fig. 4.4F). CI = 0.16, RI = 0.50. The antennomere form in Pyrgomorphidae is typically rectangular. Applying the DELTRAN optimization six transformations to quadrate antennomere occurred in: (i) the clade *Anarchita* + *Zarytes*, (ii) *Parasphena*, (iii) *Monistria*, (iv) *Dictyophorus*, (v) the clade *Sphenacris* + *Acropyrgus,* and (vi) the clade composed of *Caprorhinus*, *Pseudogeloius,* and Psednurini.

5. Head, in dorsal view, longitudinal length compared to its width: (0) longer (fig. 4.18H), (1) equal (fig. 4.18G), (2) shorter (fig. 4.18F). CI = 0.16, RI = 0.47. The head length usually is longer than its width, and it tends to be shorter in the clade B.
6. Head, in dorsal view, longitudinal length compared to longitudinal length of pronotum: (0) shorter (fig. 4.6B), (1) as long as (fig. 4.9B), (2) longer (fig. 4.6F). CI = 0.18, RI = 0.43. A shorter head is widespread across Pyrgomorphidae with independent transformations to longer heads. A shorter head is characteristic of the clade B.
7. Longitudinal length of fastigium of vertex compared to the dorsal length of eye: (0) shorter (fig. 4.18G), (1) as long as (fig. 4.18H), (2) longer (fig. 4.10F). CI = 0.27, RI = 0.38. The length of the fastigium of vertex typically is shorter than the length of eye in a dorsal view. There are cases of transformations to length of fastigium as long as the length of eye, for instance in the clade *Dictyophorus* + *Petasida*, *Sphenacris,* and the clade composed of *Caprorhinus*, *Pseudogeloius* and Psednurini.
8. Upper region of frontal ridge below fastigium, shape in lateral view: (0) rounded (fig. 4.17J), (1) sinuous (fig. 4.9A). CI = 0.33, RI = 0. The upper region of frontal ridge below fastigium usually is rounded. The sinuous condition appears independently three times (*Gymnohippus*, *Acanthopyrgus,* and *Pseudogeloius*). Those genera belong to three different tribes endemic to Madagascar.
9. Area between eyes in dorsal view (shape of vertex): (0) trapezoidal (fig. 4.18F), (1) quadrate (fig. 4.18E). CI = 1.0, RI = 1.0. The quadrate shape between the eyes is an uncontroverted synapomorphy for Chrotogonini.
10. Groove of fastigium originating from the apex in relation to the longitudinal length of fastigium: (0) extending about half way (fig. 4.9B), (1) almost touching the base, but never

actually touching the base (fig. 4.18H), (2) complete and touching the base (fig. 4.18G). CI = 0.33, RI = 0.20. The groove of fastigium usually is complete and touches the base of vertex. There is a transformation where the groove of fastigium almost touches the base of vertex. This is an uncontroverted synapomorphy for the Central American clade *Prosphena* + *Sphenarium*.

11. Head, dorsal profile from lateral view: (0) flat (fig. 4.17J), (1) concave (fig. 4.8B). UNINF. The concave condition is an autapomorphy for *Dictyophorus* but is potentially a synapomorphy for the tribe Dictyophorini.
12. Frons, surface texture: (0) smooth (fig. 4.8B), (1) with a pattern (fig. 4.8D). CI = 0.20, RI = 0.55. The frons usually possesses a patterned texture, although several members of the clade B have a smooth texture.
13. If 12:1, frons, texture: (0) foveolate (fig. 4.6D), (1) tuberculate (fig. 4.8D). CI = 0.20, RI = 0.42. When the texture of frons is patterned, it is usually fovoleate.
14. Dorsal portion of the head, surface texture: (0) smooth (fig.4. 8B), (1) with a pattern (fig. 4.8D). CI = 0.20, RI = 0.42. Most Pyrgomorphidae have the dorsal portion of the head with a patterned texture with a lot of exceptions in the clade B.
15. If 14:1, dorsal portion of the head: (0) foveolate (fig. 4.6D), (1) tuberculate (fig. 4.8D). CI = 0.33, RI = 0.60. In general, when the pattern is present, the dorsal portion of the head is foveolate. There are three independent transformations to a tuberculate texture.
16. Gena, surface texture: (0) smooth (fig. 4.8B), (1) with a pattern (fig. 4.8D). CI = 0.20, RI = 0.55. Most Pyrgomorphidae have the gena texture with a pattern. The texture of gena is usually with a pattern with a lot of exceptions in the clade B, where it is generally smooth.

17. If 16:1, gena: (0) foveolate (fig. 4.6D), (1) tuberculate (fig. 4.8D). CI = 0.50, RI = 0.66. The prevalent condition is foveolate. The tuberculate condition appears independently twice.
18. Row of tubercles between the eye and posterior border of the head in lateral view: (0) absent (fig. 4.17J), (1) present (fig. 4.4B). CI = 0.16, RI = 0.50. The majority of Pyrgomorphidae do not have a row of tubercles. The row of tubercles appears four times: (i) *Prosphena*, (ii) *Ichthyotettix*, (iii) *Caprorhinus*, and (iv) the clade D with a secondary loss in *Omura* and Chrotogonini.
19. Carinula of frontal ridge: (0) absent, (1) present (fig. 4.18C). CI = 0.50, RI = 0. The loss of this carinula occurred independently in *Aularches* and *Meubelia*.
20. If 19:1, carinula of frontal ridge: (0) complete and touching clypeus (fig. 4.18D), (1) incomplete (fig. 4.18A). CI = 0.10, RI = 0.47. The carinula of frontal ridge usually when present touches the clypeus. There are ten independent transformations to an incomplete carinula across the four main clades.
21. Ventral border of frons in lateral view: (0) ending below the eye (fig. 4.7E), (1) ending in front of eye (fig. 4.7C). CI = 1.0, RI = 1.0. The particular condition of the ventral border of frons ending in front of the eye is an uncontroverted synapomorphy of *Phymateus* and *Zonocerus* (Phymateini).
22. Eye, shape in lateral view: (0) circular (fig. 4.7C), (1) oval (fig. 4.9A). CI = 0.12, RI = 0.63.
23. Frontal sulcus, appearance: (0) faintly present, (1) well marked (fig. 4.18C). CI = 0.33, RI = 0. The frontal sulcus usually is well marked. In three instances, this state is transformed to faintly present (*Omura*, *Gymnohippus,* and *Chapmanacris*).
24. Fastigium furrow, depth: (0) shallow (fig. 4.18H), (1) deeply grooved (fig. 4.18F). CI = 1.0, RI = 1.0. The deeply grooved fastigium furrow is an uncontroverted synapomorphy for the

clade composed of *Poekilocerus*, Phymateini, *Taphronota*, *Aularches*, *Dictyophorus,* and *Petasida*.

25. Fastigial areola: (0) absent (fig. 4.18F), (1) present (fig. 4.18G). CI = 0.11, RI = 0.42. Applying the ACCTRAN optimization, the fastigial areola usually is present with six transformations to complete reduction.
26. If 25:1, fastigial areola, appearance: (0) faintly marked (fig. 4.18G), (1) well marked (fig. 4.18E). CI = 0.50, RI = 0.83. When fastigial areola is present, it is usually faintly marked. In two instances, this state is transformed to a well-marked fastigial areola: (i) *Ichthyotettix,* and (ii) in the clade composed of *Pyrgomorpha*, *Anarchita*, *Zarytes*, *Parasphena,* and Chrotogonini.
27. Carinula of fastigium of vertex: (0) absent (fig. 4.10C), (1) present (fig. 4.10B). CI = 0.50, RI = 0.50. The carinula of fastigium of vertex is typically present. Applying DELTRAN optimization, there are two independent transformations towards its absence: (i) in *Modernacris,* and (ii) in the clade *Chapmanacris* + *Meubelia*.
28. Carinula of vertex: (0) absent (fig. 4.10B), (1) present (fig. 4.19B). CI = 0.33, RI = 0.33. Most Pyrgomorphidae have the carinula of vertex, but it has been independently lost twice.
29. Occiput carinula: (0) absent (fig. 4.9B), (1) present (fig. 4.18H). CI = 0.16, RI = 0.16. The occiput carinula is usually present and applying the DELTRAN optimization it was lost four times.
30. If 28:1 & 29:1, carinula of vertex and carinula of occiput, junction: (0) not joined (fig. 4.9C), (1) joined (fig. 4.18H). UNINF. Only in *Pseudogeloius*, these two structures are not joined in the present analysis, but this character could be a synapomorphy for the tribe Geloiini.

31. Facial carina: (0) absent (fig. 4.18B), (1) present (fig. 4.18D). CI = 0.16, RI = 0.50. The facial carina typically is present. There are five instances where it is lost.
32. If 31:1, facial carina, appearance: (0) faintly marked, (1) well marked (fig. 4.18A). CI = 0.50, RI = 0.50. When facial carina is present, it is usually well marked. In two instances, this state is transformed faint marking, which is found in (i) *Mitricephaloides,* and (ii) the clade consisting of *Colemania* + *Acanthopyrgus*.
33. Groove of fastigium: (0) stopping before frons, (1) continuing to frons (fig. 4.18C). CI = 0.25, RI = 0.40. The groove of the fastigium typically continues down to frons in most species. In four cases, the groove stops before reaching frons: (i) *Anarchita*, (ii) *Taphronota*, (iii) the clade consisting of *Chapmanacris* + *Meubelia,* and (iv) the tribe Psednurini.

4.4.2.2 Pronotum

The pronotum in the clade A is simple and quadrate (34:0). In the clade B, it usually has a complex texture sometimes armed with tubercles and spines (48:1-3, 49:2 & 50:1-3). In some members of the clade D, the line of tubercles behind the eye continues towards the lateral borders of pronotum. The median carina is usually present in the clade A (39:1) whereas the lateral carina is usually present in the clades C and D (40:1). Metazona is shorter than prozona except in Chrotogonini and the great majority of the clade B (42:0). The metasternal lobe space is almost always closed in the clade A (43:0) and separated in the clades B, C, and D (43:1). The metasternal pits are usually connected in the clades B, C, D (46:1) and not connected in the clade A (46:0).

34. Pronotum, form: (0) quadrate (fig. 4.6E), (1) trapezoidal (fig. 4.6C), (2) slightly trapezoidal. CI = 0.40, RI = 0.80. The pronotum form is usually trapezoidal. There is a transformation to a quadrate pronotum in the clade A with a second transformation in *Colemania* and *Caprorhinus* to slightly trapezoidal pronotum. In the South America genus *Omura,* there is a transformation from trapezoidal pronotum to slightly trapezoidal.

35. If 34:1, pronotum form: (0) atractomorphoid, (1) zonoceroid, (2) chrotogonoid, (3) sphenarioid. CI = 0.60, RI = 0.83. The atractomorphoid state (fig. 4.4A) is characterized by well-marked lateral lobes of pronotum, and it is found in the clade D with the exception of *Omura* and Chrotogonini, as well as in *Humpatella*, *Chlorizeina* and *Desmopterella*. The zonoceroid state (fig. 4.7C) is characterized by the expansion of the metazona and absence of lateral carina, which is an uncontroverted synapomorphy of the clade composed of *Poekilocerus*, Phymateini, *Taphronota*, *Aularches*, *Dictyophorus* and *Petasida*. The chrotogonoid state (fig. 4.5D) is characterized by the lateral expansion of metazona, which is a synapomorphy for the Chrotogonini. The sphenarioid state (fig. 4.6D) is characterized by the presence of median carina, lateral carina, less marked lateral lobes of pronotum and is present in the clade C and the genus *Monistria*.

36. Posterior margin of pronotum in lateral view expands to: (0) first coxae (fig. 4.8C), (1) second coxae (fig. 4.7C), (2) third coxae (fig. 4.7E). CI = 0.33, RI = 0.76. The expansion of the posterior margin of pronotum to the first coxae is characteristic of the clade A with the exception to the genus *Mitricephaloides*. The expansion to the second coxae is found in other groups with the exception to *Omura* and the clade (*Anarchita* + *Zarytes*). The expansion to the third coxae is an autapomorphy of *Petasida* but it could be a synapomorphy of the tribe Petasidini.

37. Ventral margin of pronotum from lateral view, position: (0) above second coxae (fig. 4.7E), (1) in front second coxae (fig. 4.7D). CI = 0.50, RI = 0. The state of the position of ventral margin of pronotum from lateral view above second coxae appeared independently two times in (i) *Aularches* and (ii) *Petasida* (DELTRAN optimization).
38. If 37:1, ventral margin of pronotum from lateral view, position: (0) not cross an imaginary projection from the ventral part of lateral view to the second coxae (fig. 4.7D) (1) crosses the imaginary projection (fig. 4.8B). CI = 0.12, RI = 0.46. The ventral margin of pronotum typically does not cross an imaginary projection. They are six independently transformations to the other condition.
39. Median carina of pronotum: (0) absent (fig. 4.18I), (1) present (fig. 4.18K). CI = 0.14, RI = 0.50. The median carina of pronotum is typically present and applying the DELTRAN optimization there are five independent losses of the median carina.
40. Lateral carina of pronotum: (0) absent, (1) present. CI = 0.25, RI = 0.80. The lateral carina is present in the clade Sphenariini and in the clade D with posterior independent losses in *Pseudomorphacris* and the Chrotogonini. Another reduction of the lateral carina of pronotum appears in the clade B, the genera *Humpatella*, *Desmopterella* and the clade A. There is a regain of the lateral carina of pronotum in *Chlorizeina*.
41. Collar of prosternum: (0) absent (fig. 4.5B), (1) present (fig. 4.5D). CI = 1.0, RI = 1.0. The presence of the collar is an uncontroverted synapomorphy for the tribe Chrotogonini.
42. Metazona, length compared to prozona: (0) shorter (fig. 4.18K), (1) as long as (fig. 4.18J), (2) longer (fig. 4.18I). CI = 0.33, RI = 0.50. The length of metazona is usually shorter than prozona. Only in the 3 clades the metazona is as long as the prozona: (i) Chrotogonini, (ii) *Desmopterella*, and (iii) the clade composed of *Poekilocerus*, Phymateini, *Taphronota*,

Aularches, *Dictyophorus,* and *Petasida*. In *Zonocerus,* there is a reversal to a shorter metazona whereas in the clade of *Dictyophorus* + *Petasida* there is a transformation to a longer metazona.

43. Metasternal lobes space: (0) closed, (1) separated (fig. 4.17A). CI = 0.16, RI = 0.70. The metasternal lobes space usually is separated. There are three transformations where the space becomes closed: (i) *Anarchita*, (ii) *Monistria,* and (iii) the clade composed of *Chlorizeina*, *Desmopterella* and the clade A. There are two reversals to separated metasternal lobes space in *Ichthyotettix* and *Mitricephaloides*
44. Inner angle of metasternal lobe, form: (0) rounded (fig. 4.17A), (1) angled. CI = 0.25, RI = 0.40. The inner angle typically is rounded. Only in four independent clades there is a transformation to an angled inner angle.
45. Mesosternal lobe space, width compared to the width of each lobe: (0) shorter, (1) as wide as (fig. 4.17A), (2) longer (fig. 4.17F). CI = 0.13, RI = 0.27. Most Pyrgomorphidae have the mesosternal lobe space as wide as the width of each lobe with multiple independent transformations in the four main clades to longer and shorter than the width of each lobe.
46. Metasternal pits, connection: (0) not connected (fig. 4.17F), (1) connected (fig. 4.17A). CI = 0.25, RI = 0.76. The metasternal pits are generally connected. There are two transformations to unconnected pits in: (i) the Central American clade of *Prosphena* + *Sphenarium* and (ii) the clade A. There are two reversals to connected metasternal pits in *Meubelia* and the Psednurini.
47. Mesosternal and metasternal space, area between them, form: (0) longitudinally rectangular (fig. 4.17A), (1) quadrate (fig. 4.17F), (2) transversally rectangular. CI = 0.15, RI = 0.50.

48. Dorsal prozona, texture: (0) foveolate, (1) spinate (fig. 4.7D), (2) tuberculate (fig. 8D), (3) largely tuberculate (fig. 4.18I). CI = 0.37, RI = 0.28. The dorsal prozona usually has a fovoleate texture. There are three independent transformations to a tuberculate texture. The dorsal prozona with largely tuberculate texture is an autapomorphy of *Dictyophorus* but could be a synapomorphy of Dictyophorini.
49. Lateral pronotum, texture: (0) smooth (fig. 4.7F), (1) foveolate (fig. 4.9B), (2) tuberculate (fig. 4.5D). CI = 0.12, RI = 0.30.
50. Dorsal metazona, texture: (0) foveolate (fig. 4.18K), (1) spinate (fig. 4.7D), (2) tuberculate (fig. 4.9C), (3) with large tubercles (fig. 18I). CI = 0.37, RI = 0.28. The dorsal metazona texture generally is fovoleate with three independent transformations to tuberculate texture (DELTRAN optimization). Only *Phymateus* has the state of spinate texture.

4.4.2.3 Legs

In the clades B and C, the upper basal lobe of hind femur is shorter than the lower basal lobe (55:0). The legs in the clade B have the upper and lower marginal area in a convex shape (58:1) and the carinae and carinulae are thick (60:1). In the clade A, the internal and external spines of hind tibia are frequently only half way 64:0 & 65:0) together with clear pubescence throughout the hind tibia (67:1).

51. Fore and middle legs, condition: (0) normal (fig. 4.6C), (1) reduced (fig. 4.6E). CI = 1.0, RI = 1.0. Rentz et al. (2003) hypothesized that the reduced fore and middle legs of Psednurini might be an adaptation to living in grasslands. It is an uncontroverted synapomorphy for Psednurini.

52. Spines on fore femur: (0) absent (fig. 4.9B), (1) present (fig. 4.9A). UNINF. The presence of spines on fore femur is an autapomorphy of *Acanthopyrgus* and it could be a synapomorphy for the tribe Sagittacridini.

53. Hind femur in males, length relative to abdomen: (0) shorter (fig. 4.9F), (1) as long as (fig. 7C), (2) longer (fig. 4.6B). CI = 0.11, RI = 0.38.

54. Hind femur, ratio length:width: (0) less than 4 (fig. 4.5A), (1) more than 4 (fig. 4.5B). CI = 0.20, RI = 0.20. The ratio length:width of hind femur typically is more than 4 with four independent transformations to a ratio length:width less than 4.

55. Upper basal lobe of hind femur, length relative to lower basal lobe: (0) shorter (fig. 4.17I), (1) as long as (fig. 4.5E), (2) longer (fig. 4.5C). CI = 0.15, RI = 0.42. The plesiomorphic state is a longer upper basal lobe of hind femur compared to the lower basal lobe.

56. Outer face of hind femur, texture: (0) smooth (fig. 4.9F), (1) foveolate (fig. 4.9E). CI = 0.25, RI = 0.50. The outer face of hind femur generally has a fovoleate texture with three independent transformations to a smooth texture.

57. Hind femur, medial area dorsoventral length relative to upper and marginal area: (0) wider (fig. 4.9D), (1) equal (fig. 4.4F), (2) narrower. CI = 0.33, RI = 0.76. The dorsoventral length of the medial area of hind femur relative to upper and marginal area typically is equal. There are three independent transformations to a wider length: (i) *Tenuitarsus*, (ii) *Monistria*, and (iii) *Desmopterella* + clade A (with a reversal in *Colemania*).

58. Hind femur, upper and lower marginal area, shape: (0) concave (fig. 4.8D), (1) convex (fig. 4.7C). CI = 1.0, RI = 1.0. The state of hind femur with a convex shape is an uncontroverted synapomorphy for the clade B.

59. Hind femur, lower marginal area, dorsoventral length compared to upper marginal area: (0) wider (fig. 4.4D), (1) equal (fig. 4.5F), (2) narrower. CI = 0.22, RI = 0.36. The dorsoventral length of the lower marginal area of the hind femur typically is equal when compared to upper marginal area. There are seven transformations to a wider length.
60. Hind femur, carinae and carinulae, thickness: (0) thin (fig. 4.8E), (1) thick (fig. 4.7D). CI = 1.0, RI = 1.0. The thick carinae and carinulae in the hind femur are an uncontroverted synapomorphy for the clade B.
61. If 60:0, carinae and carinulae, pattern: (0) both carinae and carinulae same thickness (fig. 4.9B), (1) carinae thicker (fig. 4.9D), (2) carinulae thicker (fig. 4.9C). CI = 0.66, RI = 0. When carinae and carinulae are thin, they are usually of the same thickness. There is a transformation to have the carinae thicker in *Gymnohippus* that could be a synapomorphy for the tribe Gymnohippini. The same case is for the transformation to carinulae thicker that is an autapomorphy for *Pseudogeloius* but that it could be a synapomorphy for the tribe Geloiini.
62. If 60:1, carinae and carinulae, pattern: (0) both carinae and carinulae same thickness (fig. 4.8A), (1) carinae thicker (fig. 4.8B). UNINF. When carinae and carinulae are thick, they are usually of the same thickness. There is a transformation to have thicker carinae, which is an autapomorphy of *Dictyophorus* but this has the potential to be a synapomorphy for Dictyophorini.
63. Hind knee, condition: (0) dorsal and ventral lobe prominent (fig. 4.17I), (1) ventral lobe reduced (fig. 4.6F). CI = 1.0, RI = 1.0. The state of reduced ventral lobe of hind knee is an uncontroverted synapomorphy for the tribe Psednurini.

64. Hind tibiae, external spines coverage from distal to proximal part: (0) around half way (fig. 4.9D), (1) more than half way but never covering the entire tibia (fig. 4.8E), (2) covering the entire tibia (fig. 4.8D). CI = 0.22, RI = 0.56. The external spines typically cover more than half of hind tibiae from distal to proximal part, never cover the entire structure. In *Sphenacris,* the spines cover the entire tibiae, which is an autapomorphic trait, but this condition could be a synapomorphy for the tribe Ichthiacridini.
65. Hind tibiae, internal spines coverage from distal to proximal part: (0) around a half way (fig. 4.9F), (1) more than a half way but never covering the entire tibia (fig. 4.9D), (2) covering the entire tibia (fig. 4.8D). CI = 0.25, RI = 0.50. A pattern similar to the previous character is found except for the fact that *Chrotogonus*, *Aularches*, *Gymnohippus,* and *Acanthopyrgus* have the internal spines that are covering more than a half way. The genus *Sphenacris* is the only group with the internal spines that cover the entire tibiae.
66. External apical spine of hind tibiae: (0) absent (fig. 4.5D), (1) present (fig. 4.5F). CI = 0.33, RI = 0.60. This character was used extensively by Dirsh (1965) to describe the African genera.
67. Hind tibiae, pubescence: (0) very few hairs scattered through the tibiae (fig. 4.7F), (1) clearly pubescent (fig. 4.8C). CI = 0.25, RI = 0.82. The pubescence of hind tibiae typically consists of very few hairs scattered through the tibiae. There are two independent transformations to a clearly pubescent hind tibiae: (i) *Chrotogonus* and (ii) the clade A + *Desmopterella*, *Chlorizeina,* and *Humpatella* with a reversal to very few hairs in the highly modified Psednurini.
68. Second tarsomere of hind tarsi length compared to the other tarsomeres: (0) shorter (fig. 4.4B), (1) longer (fig. 4.10E), (2) equal (fig. 4.4E). UNINF. The second tarsomere of hind

tarsi is generally shorter when compared to other tarsomeres. Only the genus *Modernacris* has the second tarsomere longer than the others. This autapomorphy could be a synapomorphy for the tribe Nereniini.

69. Spurs at apical part of hind tibiae, length relative to first tarsomere: (0) shorter (fig. 4.5D), (1) longer (fig. 4.5C). UNINF. The spurs are longer only in the genus *Tenuitarsus*. This autapomorphy will be helpful to solve the internal relationships of Chrotogonini.

4.4.2.4 Wings

The wings in Pyrgomorphidae are quite diverse, and it is evident that the loss of wings occurred independently multiple times throughout the family. There are different taxonomic studies of Orthoptera that define terms such as micropterous, brachypterous, and macropterous in very different ways without common criteria (Rentz et al., 2003; Rowell, 2013; Torre-Bueno, 1989). I have adopted the following definitions for this work: (i) Micropterous tegmina refer to the condition where the first pair of wings is present, but not functional, meaning that they are attached to the body and have lost the capacity to open or move. Among the taxa included in this analysis, it is also clear that the micropterous tegmina are associated with the lack of hind wings. However, I cannot conclude that the lack of hind wings is a prerequisite for the micropterous tegmina; (ii) The term pterous is adopted here to refer to functional tegmina that are capable of opening and moving. With the current taxon sampling, the taxa with the pterous tegmina always have functional hind wings. In general the clade A is wingless (70:0) with few cases of microptery and ptery. Even in cases such as *Monistria*, *Rubellia* and *Mitricephaloides,* which have short tegmina, tegmina can open and there are functional hind wings (Dirsh, 1963; Kevan, 1963; Rentz et al., 2003). It is logical to assume that if hind wings are present, the tegmina can

open as well. Most pyrgomorphs have the pterous tegmina (71:1). In the clade D the veins are thick (76:1) and the wings slender when comparing to other clades (77:0). In the clade B the radial sector is well developed (77:1).

70. Tegmina: (0) absent (fig. 4.10D), (1) present (fig. 4.10A). CI = 0.09, RI = 0.28. Tegmina are typically present in Pyrgomorphidae, but multiple groups have lost the structure. The clade A is in general apterous with some genera that have regained tegmina. In the well-supported tribe Psednurini, which *Psedna* shows micropteryy while *Psednura* has no wings.
71. If 70:1, tegmina condition: (0) micropterous (fig. 4.6D), (1) pterous (fig. 4.6B). CI = 0.25, RI = 0.50. When the tegmina are present, they are usually pterous. The micropterous tegmina have evolved independently in the clade consisting of *Sphenarium* + *Prosphena* and *Humpatella*.
72. If 71:0, tegmina shape: (0) rounded (fig. 4.9E), (1) ovoidal (fig. 4.10C), (2) elongated (fig. 4.6D). CI = 0.66, RI = 0.50. The rounded shape of the micropterous tegmina is an autapomorphy of the genus *Caprorhinus*. The ovoidal shape appears independently in the genera *Humpatella*, *Meubelia,* and *Psedna*. The ovoidal shape is a synapomorphy of the Central American clade of *Prosphena* + *Sphenarium*.
73. If 71:0, tegmina color: (0) similar to the rest of the body (fig. 4.5F), (1) contrasting from the rest of the body (fig. 4.10C). CI = 0.50, RI = 0. *Meubelia* and *Caprorhinus* have the tegmina that are clearly contrasting from the coloration of abdomen and pronotum.
74. If 71:1, tegmina polymorphism: (0) absent (fig. 4.7D), (1) present (fig. 4.6B). CI = 0.50, RI = 0. Both *Monistria* and *Rubellia* show wing length polymorphism from fully winged to reduced tegmina (but still functional, see character 71). In several species of *Monistria*,

there is even wing polymorphism within the same population (Rentz et al., 2003). There is also evidence of wing polymorphism in other species, such as *Chrotogonus hemipterus* (Blackith & McE, 1967), *Psedna nana* (Rentz et al., 2003) and *Zonocerus variegatus* (Chapman et al., 1986).

75. If 71:1, dark dot on the base of tegmina: (0) absent (fig. 4.7B), (1) present (fig. 4.4D). CI = 0.50, RI = 0. Usually the petrous tegminal have a transparent base. In the clade B, *Tagasta* and *Pseudomorphacris* have dark dots on the base of tegmina.
76. If 71:1, thickness of veins: (0) thin (fig. 4.7D), (1) thick (fig. 4.4C). CI = 0.50, RI = 0.87. When pterous, the veins are usually thin. There are two independent transformations to thick veins in: (i) *Chlorizeina,* and (ii) the clade B (with multiple losses of tegmina in this clade).
77. If 71:1, radial sector (Rs) development: (0) poorly developed (fig. 4.4A), (1) well developed (fig. 4.7A). CI = 0.33, RI = 0.77. There are two transformations to tegmina with well developed radial sector: (i) *Rubellia* and (ii) the clade D.
78. If 71:1, first part of precostal area, development: (0) poorly developed (fig. 4.7B), (1) well developed (fig. 4.7A). CI = 1.0, RI = 1.0. Typically the first part of precostal area is poorly developed in pterous tegmina, but there is a transformation to well-developed precostal area in the clade consisted of the genera *Aularches*, *Dictyophorus,* and *Petasida*. This is an uncontroverted synapomorphy for the clade.
79. If 71:1, cells of tegmina, shape: (0) quadrate to penta-hexagonal (fig. 4.7E), (1) rectangular (fig. 4.7D). CI = 0.33, RI = 0.60. When pterous, the cells of tegmina are typically rectangular. There are two transformations to tegmina with cells quadrate to penta-

hexagonal in shape: (i) *Monistria* and (ii) the clade consisted of *Taphronota*, *Aularches*, *Dictyophorus,* and *Petasida*.

80. If 71:1, tubercles on tegmina: (0) absent (fig. 4.5E), (1) present (fig. 4.5C). CI = 1.0, RI = 1.0. The pterous tegmina usually have no tubercles, but there is a transformation to have tubercles on tegmina, which is an uncontroverted synapomorphy for Chrotogonini.
81. If 71:1, tegmina overlapping at base: (0) overlaps (fig. 4.7D), (1) not overlaps (fig. 4.7C). UNINF. The pterous tegmina generally overlap at base. *Zonocerus* is the only genus to have the tegmina that do not overlap.
82. Hind wings: (0) absent (fig. 4.6D), (1) present (fig. 4.8A). CI = 0.12, RI = 0.66. In all genera with the pterous tegmina sampled in this study, the hind wings are present.
83. If 82:1, hind wing color: (0) transparent (fig. 4.4D), (1) colored (fig. 4.8A). CI = 0.33, RI = 0.71. When hind wings are present, they are usually colored. There are two independent transformations to transparent hind wings: (i) *Desmopterella* and (ii) the clade consisted of *Schulthessia*, *Omura, Pseudomorphacris*, *Pyrgomorpha*, *Anarchita*, *Zarytes*, *Parasphena,* and Chrotogonini.

4.4.2.5 Abdomen

The abdomen in Pyrgomorphidae is very consistent throughout the family. In the clade A, there are some modifications, such as an inflated middle dorsal area of last abdominal tergite (84:1) and protruded lateral posterior borders (90:1). Also in the clade A, the cerci are elongated in several groups (87:0), contrary to conical (87:1) or triangular (87:2) shapes found in other clades. The presence of the mid-dorsal abdominal gland (92:1) is a unique feature within Orthoptera,

and it is present in the clades A and B. The contrasting color pattern (alternation of dark and light bands) is found mainly in the clade B (93:1).

84. Last abdominal tergite, shape of middle dorsal area: (0) flat (fig. 4.8D), (1) inflated (fig. 4.8C). CI = 0.25, RI = 0.25. The shape of middle dorsal area of last abdominal tergite generally is flat. Applying the DELTRAN optimization, there are four independent transformations to an inflated shape.
85. Last abdominal sternite, upper lateral angles: (0) not angled (fig. 4.9E), (1) angled (fig. 4.9F). UNINF. Dirsh (1965) mentioned that the angled upper lateral last sternite is characteristic for *Chapmanacris*. This autapomorphy could be a synapomorphy for the tribe Chapmanacridini.
86. Distance betweeen the base of cerci and epiproct, position: (0) nearly adjacent (fig. 4.17E), (1) separated (fig. 4.8C). CI = 0.14, RI = 0.53. The cerci and epiproct are usually nearly adjacent at the base. There are three independent transformations where the cerci and epiproct are separated. (DELTRAN optimization).
87. Cerci, shape: (0) elongated (fig. 4.10B), (1) conical (fig. 4.4C), (2) triangular (fig. 4.17E), (3) complex (fig. 4.9C). CI = 0.27, RI = 0.57. The shape of the cerci is typically conical in Pyrgomorphidae. There are three transformations to elongated cerci (all in the clade A). There are five transformations to triangular cerci. Finally, there is a transformation to complex cerci in *Pseudogeloius*.
88. Posterior margin of the last abdominal tergite, shape of border: (0) flat (fig. 4.17C), (1) concave (fig. 4.17H), (2) almost divided (fig. 4.5F). CI = 0.28, RI = 0.75. The posterior margin of the last abdominal tergite usually has a concave border. There are two

transformations to a flat border: (i) Chrotogonini and (ii) the clade B. Additionally, there is a transformation to an almost divided border (*Humpatella* and *Chlorizeina*) with another transformation to the flat border in the clade *Desmopterella* and the clade A. In the clade A, there are three independent reversals to the concave border.

89. Last abdominal tergite, shape of the posterior corners of dorsal area: (0) flat (fig. 4.17E), (1) protruded (fig. 4.17H). CI = 0.12, RI = 0.63. The shape of the posterior corners of dorsal area of last abdominal tergite is usually flat. There are six transformations to protruded posterior corners.

90. Last abdominal tergite, shape of lateral posterior borders: (0) flat (fig. 4.10C), (1) protruded (fig. 4.10E). CI = 1.0, RI = 1.0. The shape of lateral posterior borders of the last abdominal tergite is usually flat. There is a single transformation to protruded lateral posterior borders in the clade *Mitricephaloides* + *Modernacris*.

91. Subgenital plate, length: (0) short (fig. 4.6D), (1) long (fig. 4.6E). CI = 0.50, RI = 0.50. The length of subgenital plate is generally short with a single transformation to elongated subgenital plate in Psednurini.

92. Mid-dorsal abdominal gland: (0) absent, (1) present. CI = 0.33, RI = 0.33. In general, pyrgomorphs do not possess a mid-dorsal abdominal gland. Applying the ACCTRAN optimization there are two independent origins of the mid-dorsal abdominal gland: (i) *Colemania* and (ii) the clade consisting of *Poekilocerus*, Phymateini, *Taphronota*, *Aularches*, *Dictyophorus,* and *Petasida*. Later there was a loss of the mid-dorsal abdominal gland in the clade consisted of *Taphronota*, *Aularches*, *Dictyophorus,* and *Petasida*. It is important to point out that *Taphronota* and *Aularches* have dorsal openings in the pronotum and abdomen, and *Dictyophorus* and *Taphronota* can release foams using a combination of

air from spiracles and hemolymph. *Petasida* is known to feed on toxic plants, but does not produce toxic foams (Rentz et al., 2003).

93. Abdomen coloration, pattern: (0) uniform (fig. 4.4C), (1) contrasting (fig. 4.7D). CI = 0.50, RI = 0.87. I defined contrasting coloration as the pattern of colors that is alternating between light and dark colors. The abdomen coloration typically is uniform in most pyrgomorphs. There are two transformations to contrasting abdomen coloration: (i) *Colemania* in the clade A and (ii) the clade D.

4.4.2.6 Male genitalia

Six out of the seven uncontroverted synapomorphies for the Pyrgomorphidae are from the male genitalia, three from the epiphallus (94:1, 95:0 & 96:1), one from the ectophallus (105:1), and two from the endophallus (117:0 & 118:0). Kevan (1976) and Kevan et al. (Kevan et al., 1969, 1970, 1971, 1972, 1974, 1975) based their entire classification scheme on the inner genitalia. The general structure of the inner male genitalia is consistent with modifications mainly in the clades A & D (Figs 11-16). The most important and conspicuous characteristic is that in ectophallus the cingulum reaches the ventral side enveloping the endophallus (105:1) (Figs 15 and 16).

Epiphallus

94. Epiphallus, posterior projections: (0) absent, (1) present. CI = 1.0, RI = 1.0. The presence of posterior projections is an uncontroverted synapomorphy for the family Pyrgomorphidae.
95. Epiphallus, ancorae: (0) absent, (1) present. CI = 1.0, RI = 1.0. The absence of ancorae in the epiphallus is a synapomorphy for the Pyrgomorphidae (Kevan et al. 1969)

96. Oval sclerites, shape: (0) oval, (1) club-shaped (fig. 4.13D). CI = 1.0, RI = 1.0. Despite the name, the oval sclerites in Pyrgomorphidae are club-shaped and this is a synapomorphy for the family.

97. Externo-lateral expansions of lateral plates of epiphallus: (0) absent, (1) present (fig. 4.13A). CI = 0.50, RI = 0.85. The lateral plates of epiphallus usually lack externo-lateral expansions. There are two independent transformations where the externo-lateral expansions develop: (i) *Aularches,* and (ii) the clade consisted of *Schulthessia*, *Pyrgomorpha*, *Anarchita*, *Zarytes*, *Parasphena* and Chrotogonini.

98. Bridge of epiphallus, shape: (0) unconstricted (fig. 4.11C), (1) constricted (fig. 4.11B). CI = 0.33, RI = 0. The bridge of epiphallus typically is unconstricted. There are three genera where the bridge of epiphallus is constricted: *Tagasta*, *Humpatella,* and *Chlorizeina*.

99. Epiphallus, general shape: (0) quadrate (fig. 4.11D), (1) rectangular (fig. 4.11G). CI = 0.50, RI = 0.90. The general shape of epiphallus is usually quadrate with two independent transformations to a rectangular shape: (i) the clade consisted of *Schulthessia*, *Pyrgomorpha*, *Anarchita*, *Zarytes*, *Parasphena* and Chrotogonini, and (ii) the clade C.

100. Lophi, shape: (0) short (fig. 4.12J), (1) elongated (fig. 4.12I). CI = 0.33, RI = 0.33. The majority of Pyrgomorphidae have short lophi. There are three independent transformations to elongated lophi, all in the clade A: (i) *Gymnohippus*, (ii) *Meubelia*, and (iii) *Colemania* + *Acanthopyrgus*.

101. Epiphallus, size relative to genital capsule (ectophallus + endophallus): (0) smaller (fig. 4.13C), (1) larger (fig. 4.13D). CI = 0.50, RI = 0. The size of epiphallus is typically smaller than the genital capsule. There are two genera of the clade B where the epiphallus is larger than the genital capsule: *Poekilocerus* and *Phymateus*.

102. Bridge, lateral plates and lophi, condition: (0) separated, (1) fused (fig. 4.11A). UNINF. The plesiomorphic condition in Pyrgomorphidae is a separated lateral plates and lophi. The fusion of those parts is an autapomorphy of *Atractomorpha*, and this character could be a synapomorphy for the Atractomorphini.
103. Lateral plates, condition: (0) separated, (1) fused in the middle (fig. 4.13I). UNINF. The fusion of the lateral plates is an autapomorphy for *Ichthyotettix*. It could be a synapomorphy for the tribe Ichthyotettigini.
104. Number of lobes in lophi: (0) one, (1) two. UNINF. The presence of two lobes in the lophi is an autapomorphy for the genus *Pseudomorphacris*.

Ectophallus

105. Cingulum, extension: (0) only on dorsal side, (1) reaching ventral side enveloping endophallus. CI = 1.0, RI = 1.0. Kevan et al. (1969) and Eades (2000) mentioned the characteristic cingulum in Pyrgomorphidae that reaches the ventral side enveloping the endophallus. This is an uncontroverted synapomorphy for the family.
106. Valves of cingulum: (0) absent, (1) present. CI = 0.33, RI = 0.50. The valves of cingulum are typically present in the family, but it has been lost twice independently: (i) Psednurini and (ii) *Monistria*.
107. Zygoma, size: (0) reduced: (1) normal (fig. 4.12E), (2) covering the entire dorsal area (fig. 4.12I). UNINF. The size of zygoma usually is normal (Figs 4.11-4.14). The reduced zygoma is an autapomorphy of *Modernacris* and the zygoma covering the entire dorsal area is an autapomorphy of *Gymnohippus*. In both cases the inclusion of more genera could

convert this autapomorphies into synapomorphies for the tribes Nereiniini and Gymnohippini respectively.

108. Central membrane of ectophallus: (0) absent (fig. 4.14A), (1) present (fig. 4.13D). CI = 0.50, RI = 0. There are two independent losses of the central membrane: (i) *Gymnohippus* and (ii) *Acanthopyrgus*.

109. Supra zygomal plate: (0) absent, (1) present (fig. 4.15C). CI = 0.16, RI = 0.37. The supra zygomal plate is usually present. There are five losses of the supra zygomal plate. (DELTRAN optimization).

110. Ridge of cingulum: (0) absent, (1) present (fig. 4.12D). CI = 0.16, RI = 0.44. The ridge of cingulum is typically absent with five independent gains.

111. Ventral processes of cingulum: (0) absent, (1) present. UNINF. The ventral processes of cingulum are generally present. The absence of ventral processes of cingulum is an autapomorphy of *Gymnohippus*. The inclusion of other genera of Gymnohippini will help us to determine if this condition is a synapomorphy for the tribe.

112. If 111:1, ventral processes of cingulum: (0) vestigial, (1) reduced, (2) well developed (fig. 4.15C). CI = 0.25, RI = 0.14. When the ventral processes of cingulum are present, they are generally well developed. There are five transformations to the reduced processes of cingulum.

113. Apodemal plates of cingulum, shape: (0) elongated (fig. 4.14G), (1) rounded (fig. 4.15C), (2) inflated. CI = 0.66, RI = 0. The shape of the apodemal plates of cingulum is usually rounded. In two independent clades, there is a transformation to elongated shape (*Ichthyotettix* and *Meubelia*). In *Modernacris* there is a transformation to inflated apodemal plates.

Endophallus

114. Sclerite division (basal and apical valves) of endophallus: (0) absent, (1) present. CI = 0.50, RI = 0. Eades (2000) stated that the condition of endophallus as a single unit without the division into basal and apical valves is one of the synapomorphies for Pyrgomorphidae.
115. Ventral processes of endophallic apodeme: (0) absent (fig. 4.16B), (1) present. CI = 0.25, RI = 0. The ventral processes of endophallic apodeme are generally absent with four independent transformations where the ventral processes develop.
116. Dorsal posterior processes of endophallic apodeme: (0) absent (fig. 4.16B), (1) present. CI = 0.11, RI = 0.33. The dorsal posterior processes of endophallic apodeme are typically absent, but evolved independently six times.
117. Endophallic apodeme, position: (0) medially (fig. 4.116D), (1) laterally. CI = 1.0, RI = 1.0. The medial position of endophallic apodeme is a synapomorphy proposed by Eades (2000) for Pyrgomorphidae.
118. Gonopore development relative to ejaculatory sac and sperm sac: (0) unconstricted, (1) constricted. CI = 1.0, RI = 1.0. The unconstricted ejaculatory sac and spermatophore sac is also a synapomorphy for Pyrgomorphidae (Eades, 2000).

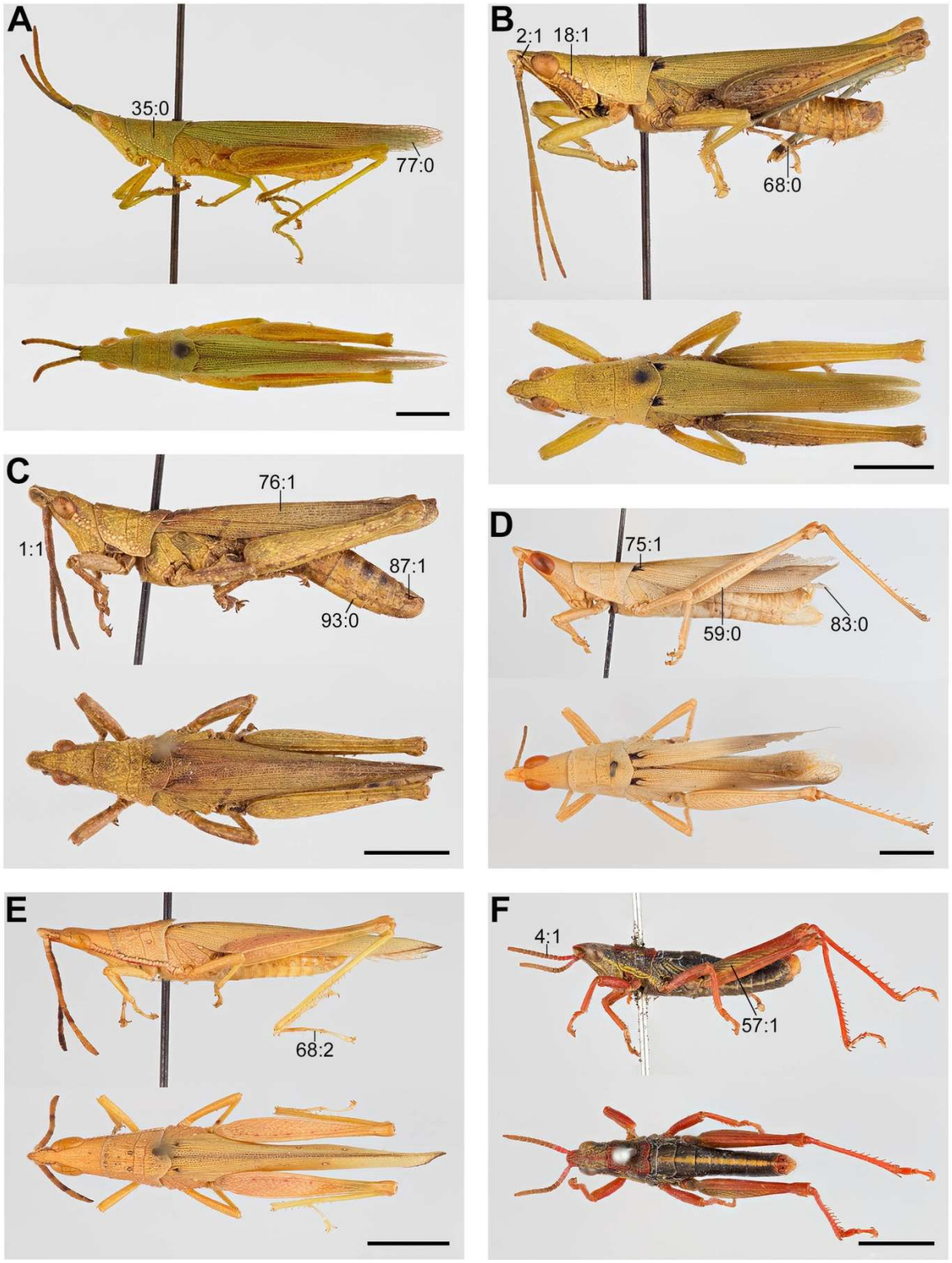

Figure 4.4. Lateral and dorsal views of Pyrgomorphidae 1. A. *Atractomorpha aberrans* (Congo); B. *Tagasta indica* (India); C. *Pyrgomorpha vignaudi* (Central African Republic); D. *Pseudomorphacris notata* (Myanmar); E. *Schulthessia biplagiata* (Madagascar) and F. *Parasphena imatogensis* (Sudan). Scale bar = 5 mm.

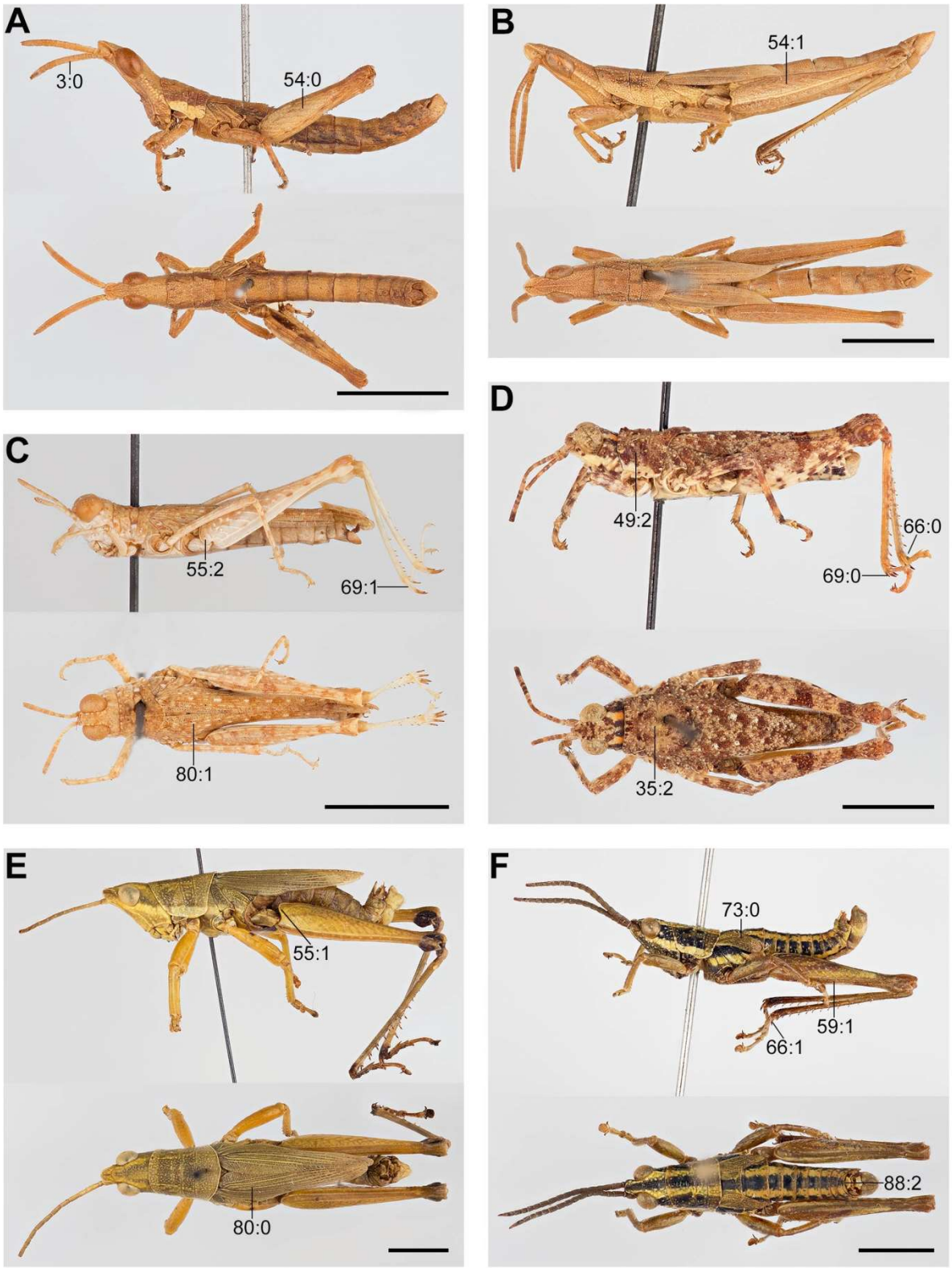

Figure 4.5. Lateral and dorsal views of Pyrgomorphidae 2. A. *Anarchita aptera* (India); B. *Zarytes squalinus* (India); C. *Tenuitarsus angustus* (Mauritania); D. *Chrotogonus oxypterus* (India); E. *Chlorizeina unicolor* (Thailand) and F. *Humpatella huambae* (Angola). Scale bar = 5 mm.

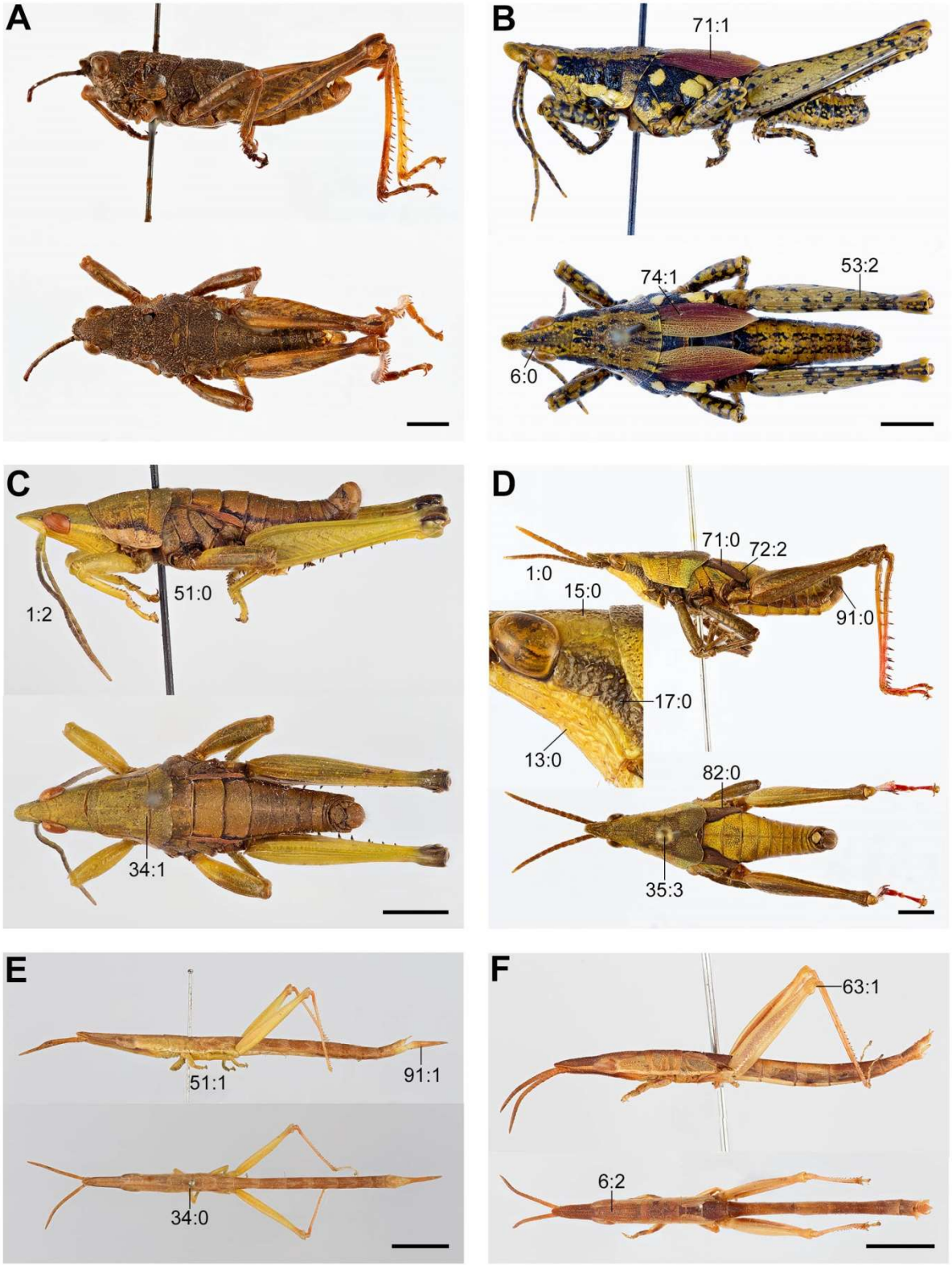

Figure 4.6. Lateral and dorsal views of Pyrgomorphidae 3. A. *Mekongiella kingdoni* (China); B. *Rubellia nigrosignata* (Madagascar); C. *Sphenarium histrio* (Mexico); D. *Prosphena scudderi* (Guatemala); E. *Psednura musgravei* (Australia) and F. *Psedna nana* (Australia) Scale bar = 5 mm.

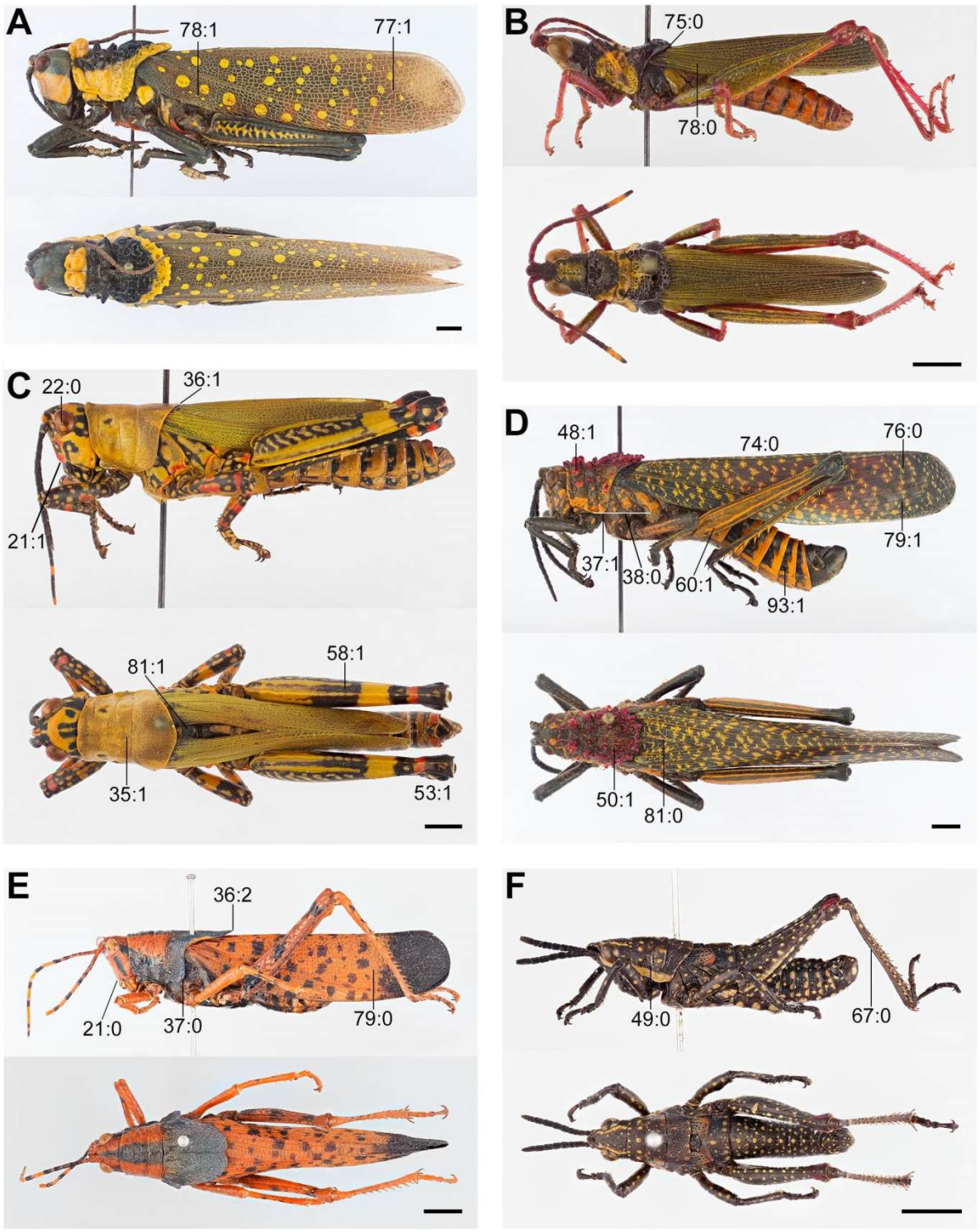

Figure 4.7. Lateral and dorsal views of Pyrgomorphidae 4. A. *Aularches miliaris* (Thailand); B. *Taphoronota ferruginea* (Cameroon); C. *Zonocerus variegatus* (Congo); D. *Phymateus saxosus* (Madagascar); E. *Petasida ephippigera* (Australia) and F. *Monistria concinna* (Australia). Scale bar = 5 mm.

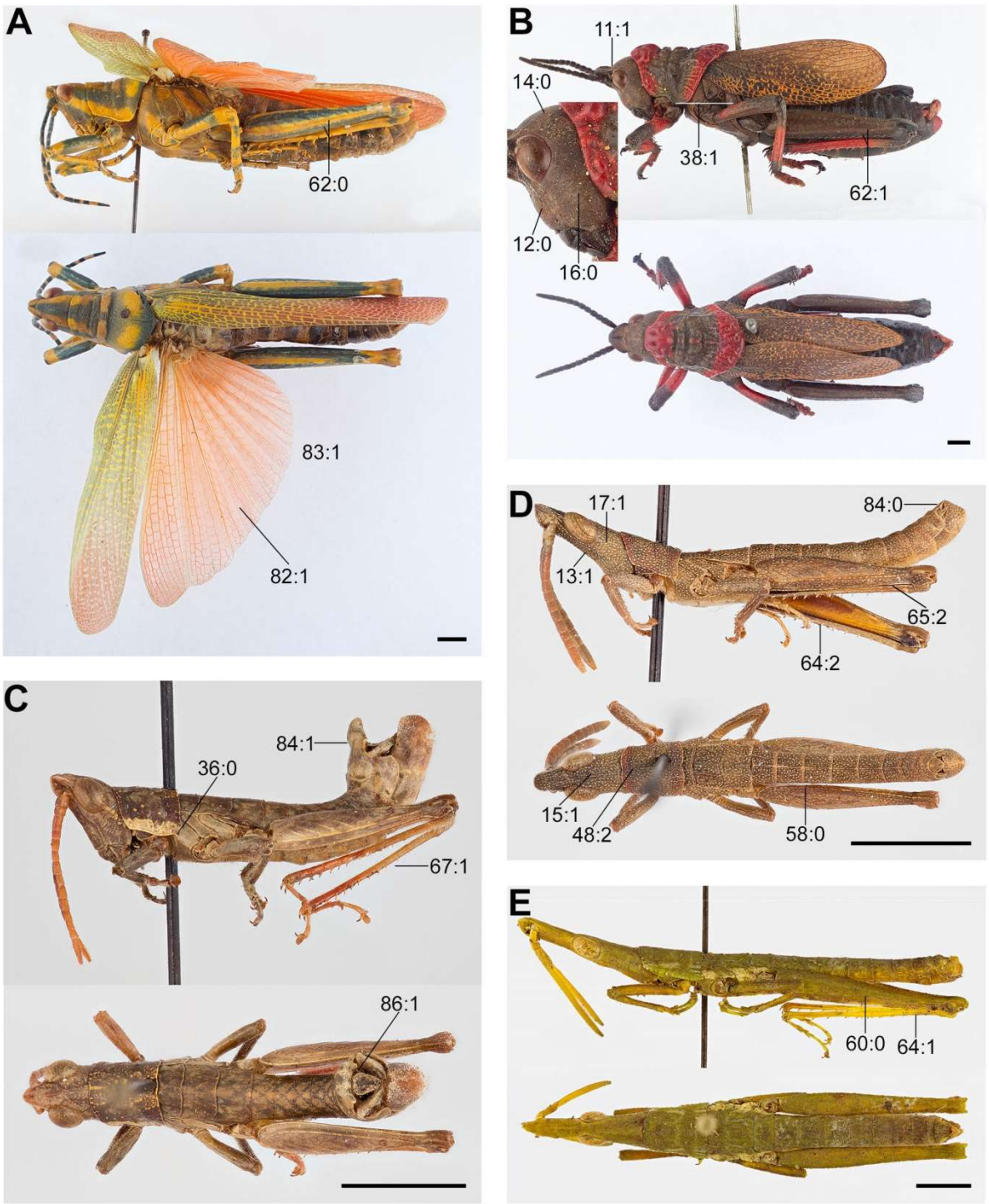

Figure 4.8. Lateral and dorsal views of Pyrgomorphidae 5. A. *Poekilocerus pictus* (India). B. *Dictyophorus spumans* (South Africa). C. *Ichthyotettix mexicanus* (Mexico). D. *Sphenacris crassicornis* (Mexico). E. *Omura congrua* (Peru). Scale bar = 5 mm.

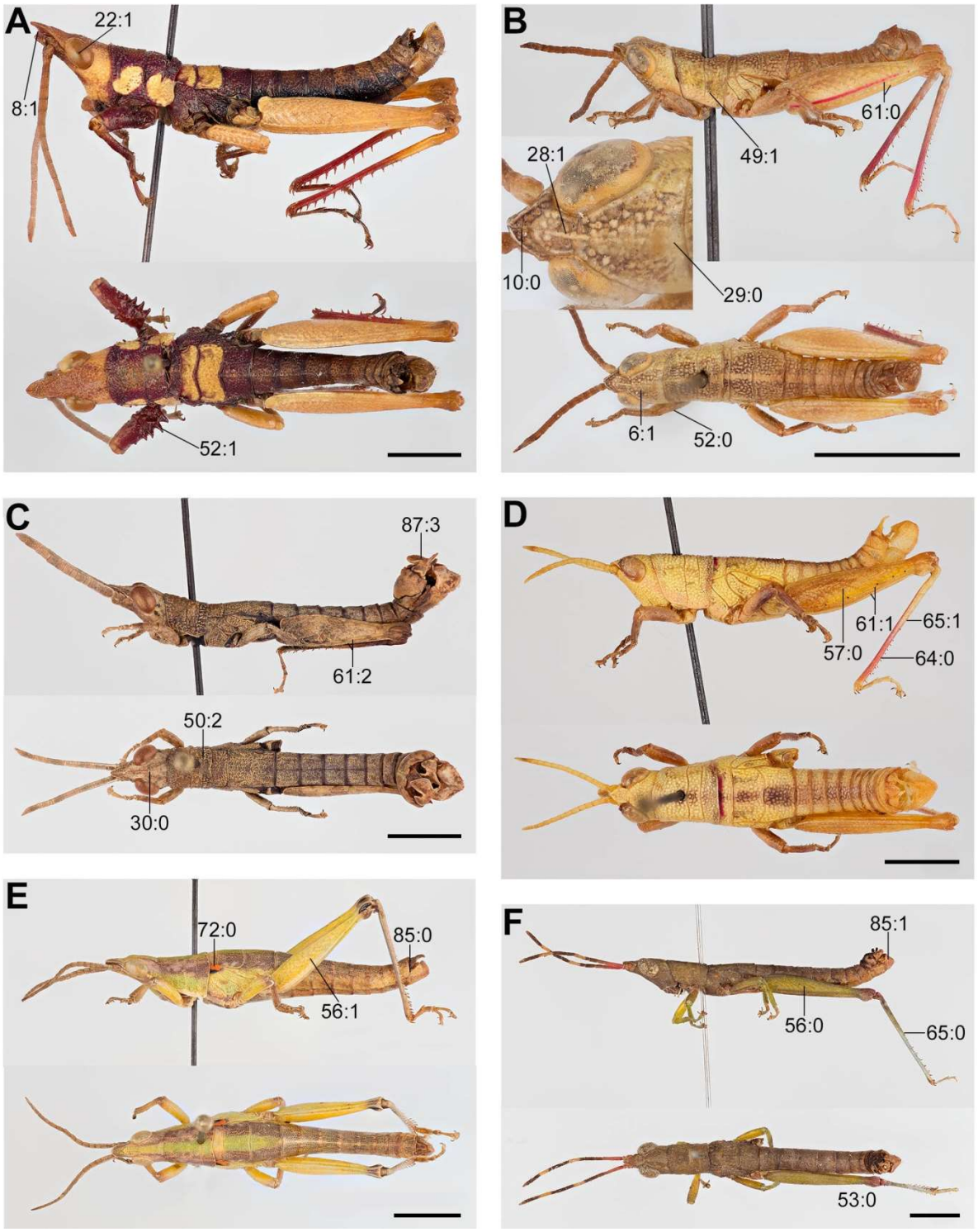

Figure 4.9. Lateral and dorsal views of Pyrgomorphidae 6. A. *Acanthopyrgus finoti* (Madagascar); B. *Acropyrgus cadeti* (Madagascar); C. *Pseudogeloius decorsei* (Madagascar); D. *Gymnohippus marmoratus* (Madagascar); E. *Caprorhinus kevani* (Madagascar) and F. *Chapmanacris sylvatica* (Ghana). Scale bar = 5 mm.

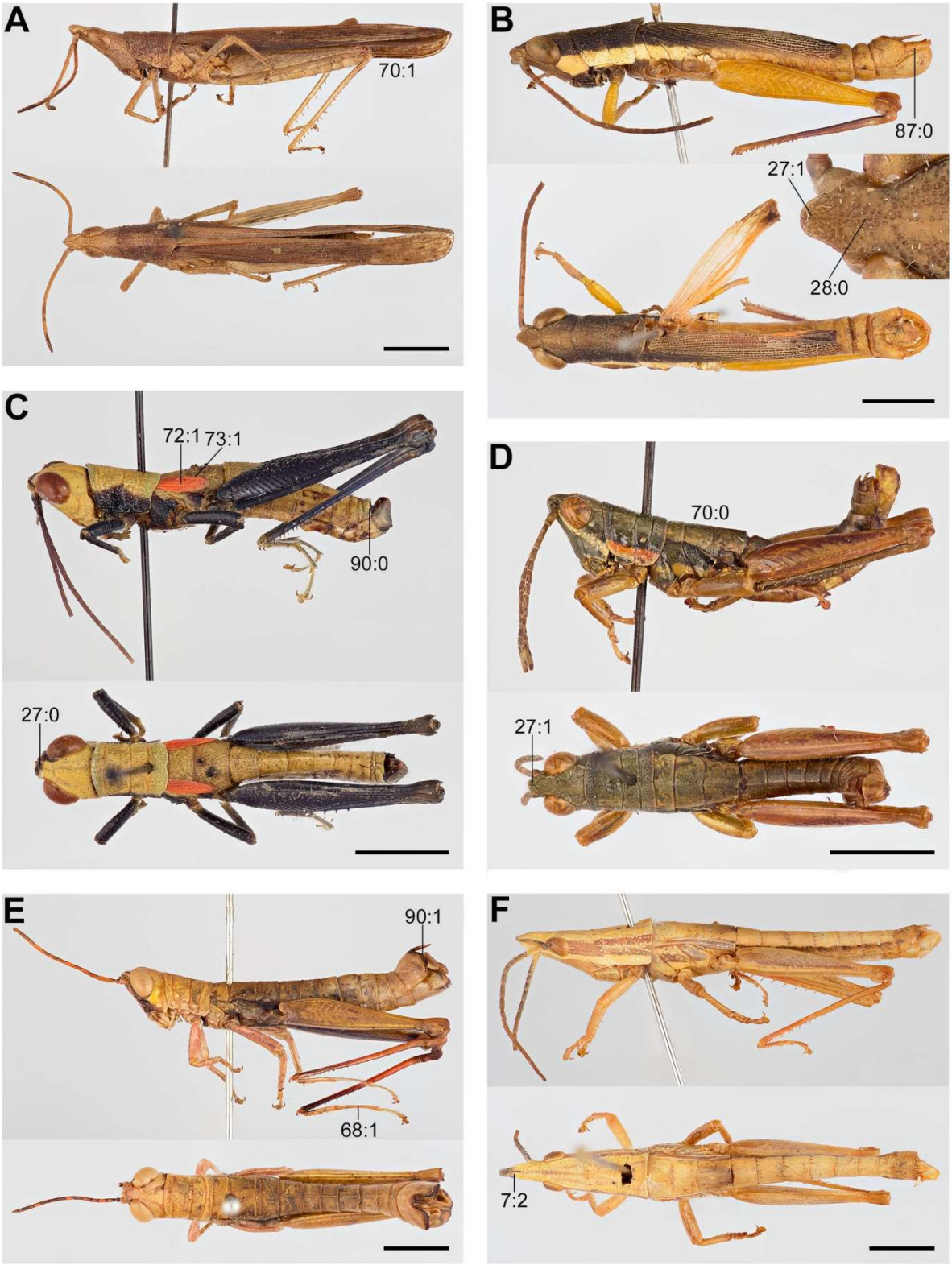

Figure 4.10. Lateral and dorsal views of Pyrgomorphidae 7. A. *Desmopterella angustata* (Papua New Guinea); B. *Mitricephaloides rhodopterus* (Malaysia); C. *Meubelia leytensis* (Philippines); D. *Orthacris incongruens* (India); E. *Modernacris controversa* (Solomon Islands) and F. *Colemania sphenarioides* (India). Scale bar = 5 mm.

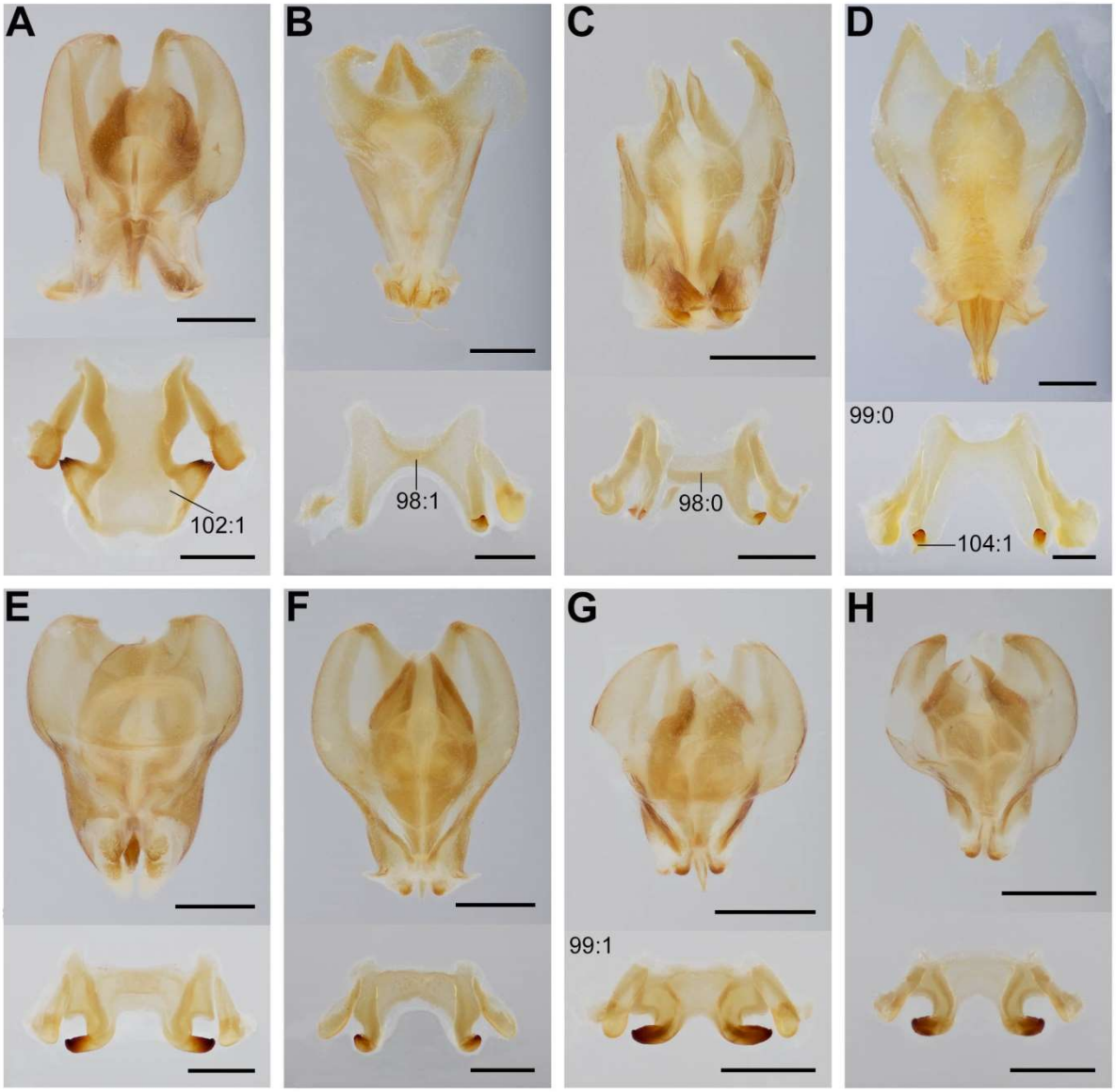

Figure 4.11. Ectophallus + endophallus and epiphallus in dorsal view of Pyrgomorphidae 1. A. *Atractomorpha aberrans* (Congo); B. *Tagasta indica* (India); C. *Schulthessia biplagiata* (Madagascar); D. *Pseudogeloius decorsei* (Madagascar); E. *Pyrgomorpha vignaudi* (Central African Republic); F. *Parasphena imatogensis* (Sudan); G. *Anarchita aptera* (India) and H. *Zarytes squalinus* (India). Scale bar = 0.5 mm.

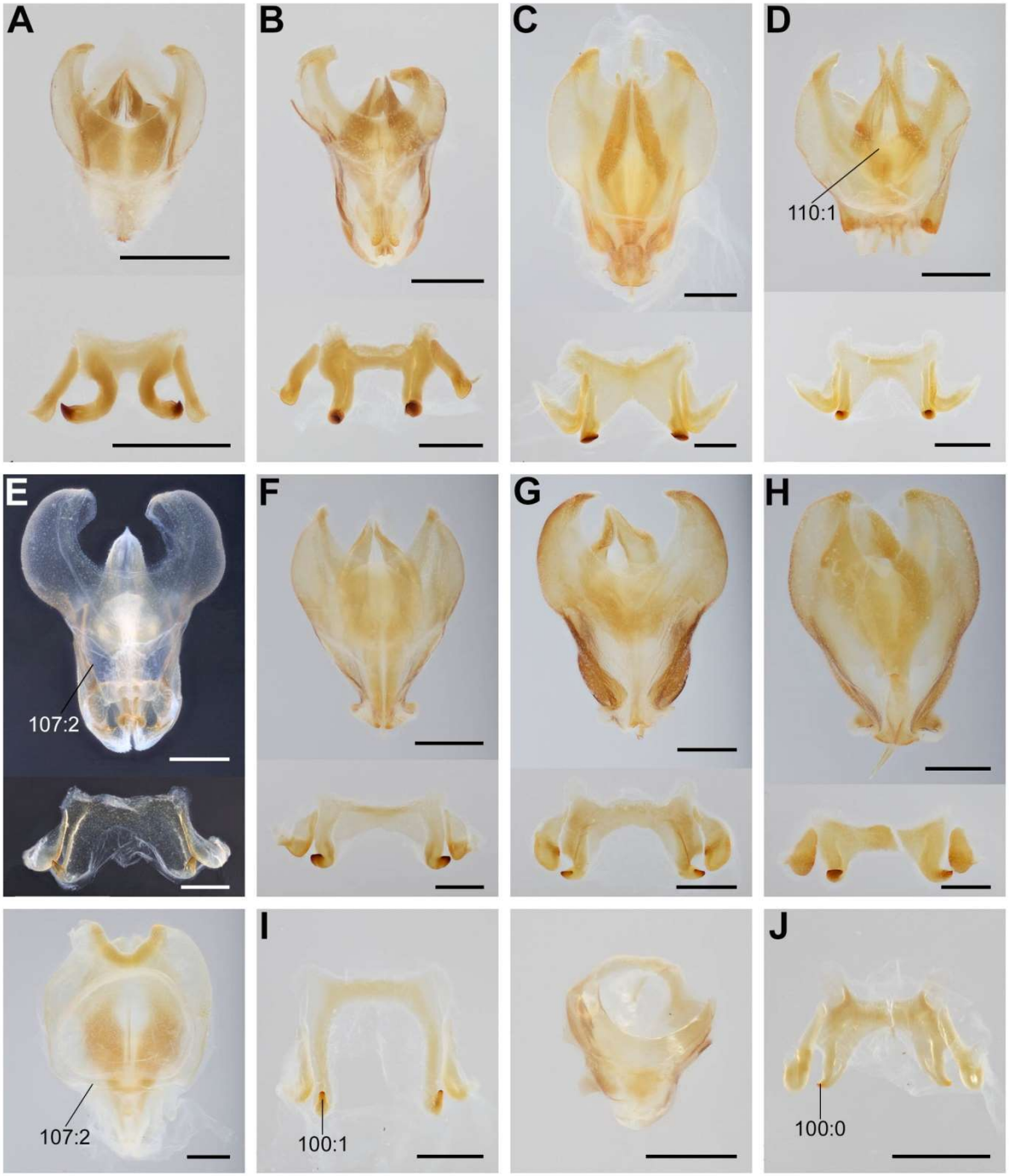

Figure 4.12. Ectophallus + endophallus and epiphallus in dorsal view of Pyrgomorphidae 2. A. *Tenuitarsus angustus* (Mauritania); B. *Chrotogonus oxypterus* (India); C. *Chlorizeina unicolor* (Thailand); D. *Humpatella huambae* (Angola); E. *Mekongiella kingdoni* (China); F. *Rubellia nigrosignata* (Madagascar); G. *Sphenarium histrio* (Mexico); H. *Prosphena scudderi* (Guatemala); I. *Gymnohippus marmoratus* (Madagascar) and J. *Acropyrgus cadeti* (Madagascar). Scale bar = 0.5 mm.

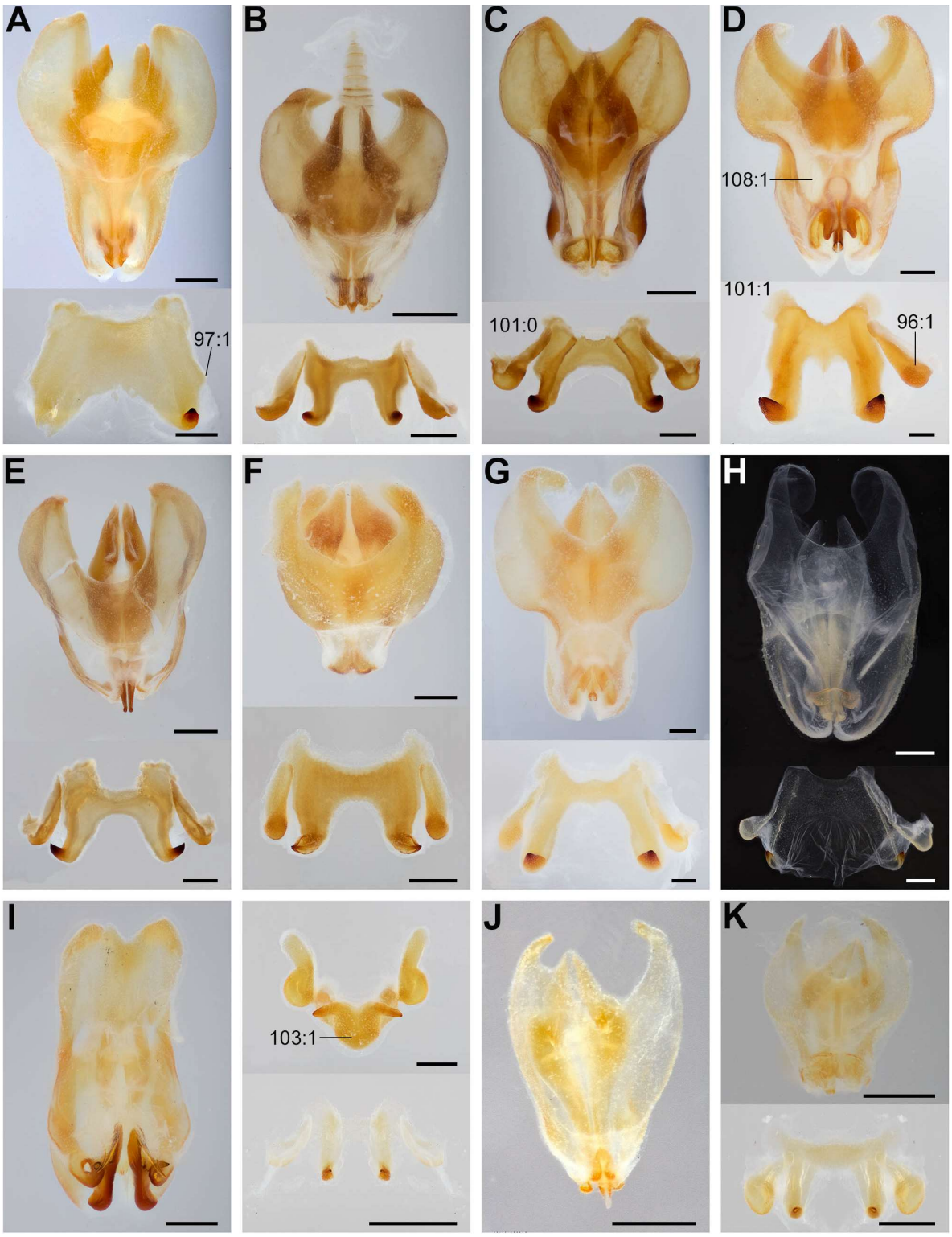

Figure 4.13. Ectophallus + endophallus and epiphallus in dorsal view of Pyrgomorphidae 3. A. *Aularches miliaris* (Thailand); B. *Taphoronota ferruginea* (Cameroon); C. *Zonocerus variegatus* (Congo); D. *Phymateus saxosus* (Madagascar); E. *Petasida ephippigera* (Australia); F. *Monistria concinna* (Australia); G. *Poekilocerus pictus* (India); H. *Dictyophorus spumans* (South Africa); I. *Ichthyotettix mexicanus* (Mexico); J. *Sphenacris crassicornis* (Mexico) and K. *Orthacris incongruens* (India). Scale bar = 0.5 mm.

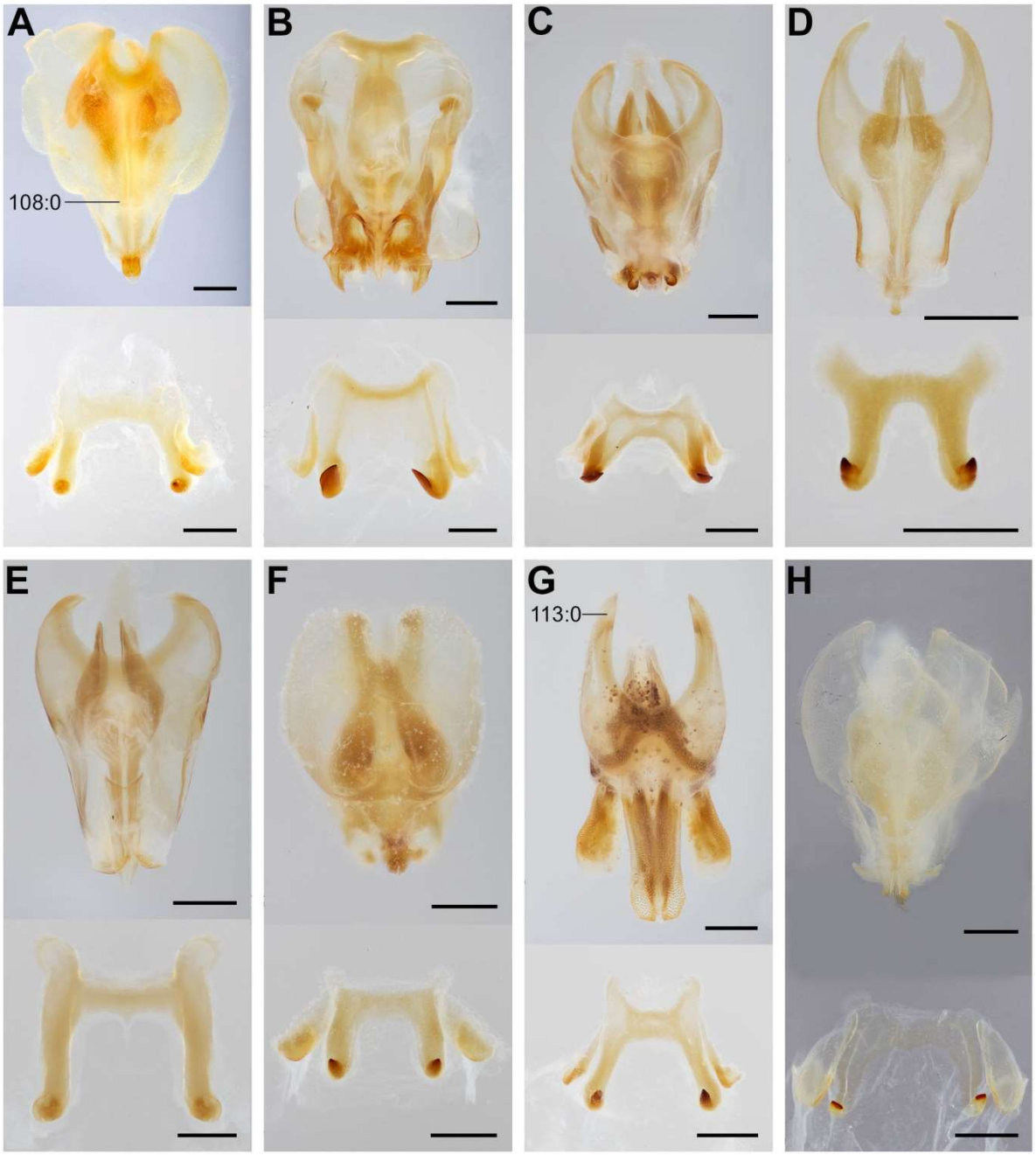

Figure 4.14. Ectophallus + endophallus and epiphallus in dorsal view of Pyrgomorphidae 4. A. A*canthopyrgus finoti* (Madagascar); B. *Pseudogeloius decorsei* (Madagascar); C *Chapmanacris sylvatica* (Ghana); D. *Psednura musgravei* (Australia); E. *Omura congrua* (Peru); F. *Desmopterella angustata* (Papua New Guinea); G. *Meubelia leytensis* (Philippines) and H. *Colemania sphenarioides* (India). Scale bar = 0.5 mm.

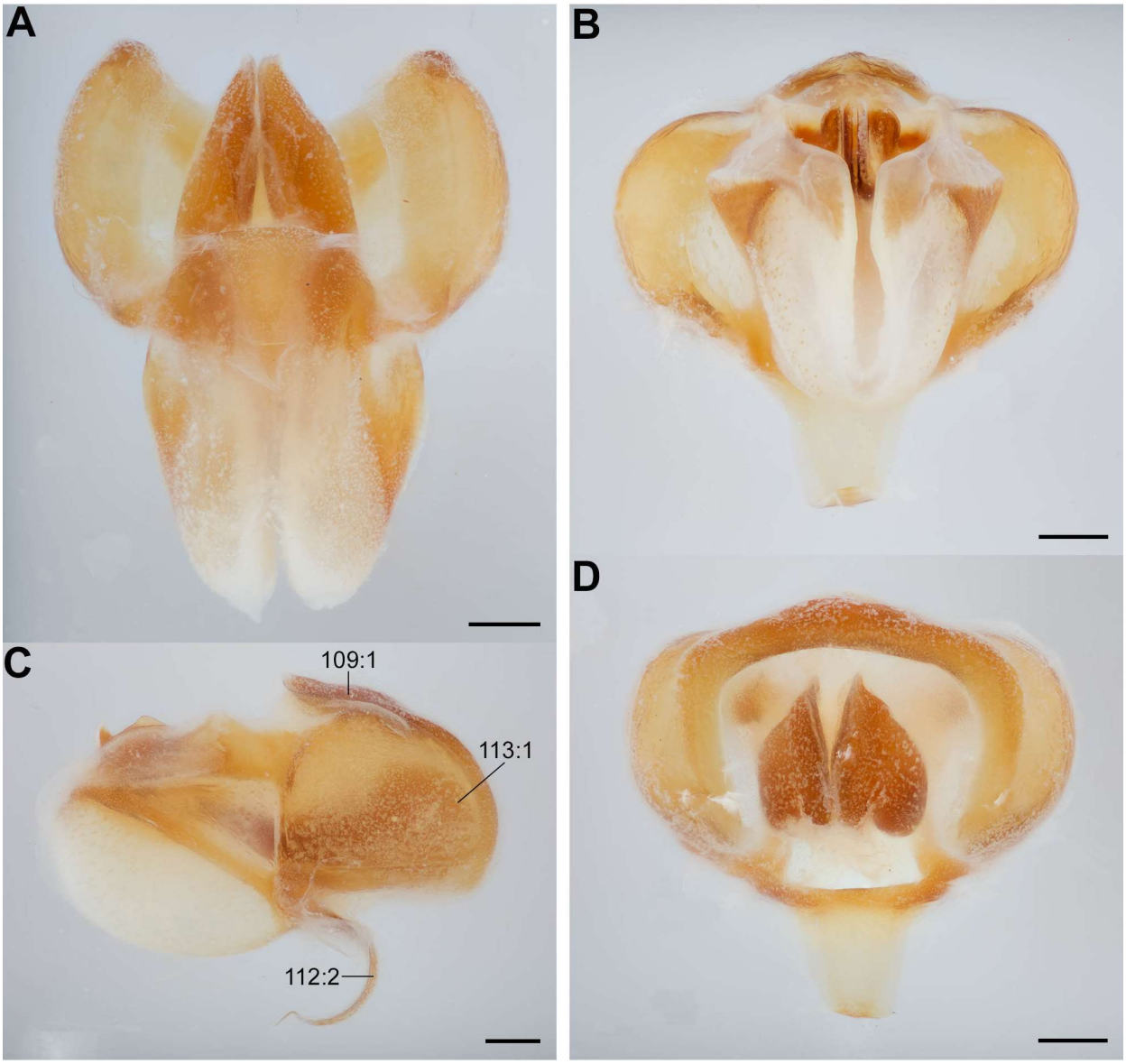

Figure 4.15. Ectophallus + Endophallus of *Phymateus saxosus* (Madagascar). A. Ventral view; B. Posterior view; C. Lateral view and D. Anterior view. Scale bar = 0.5 mm.

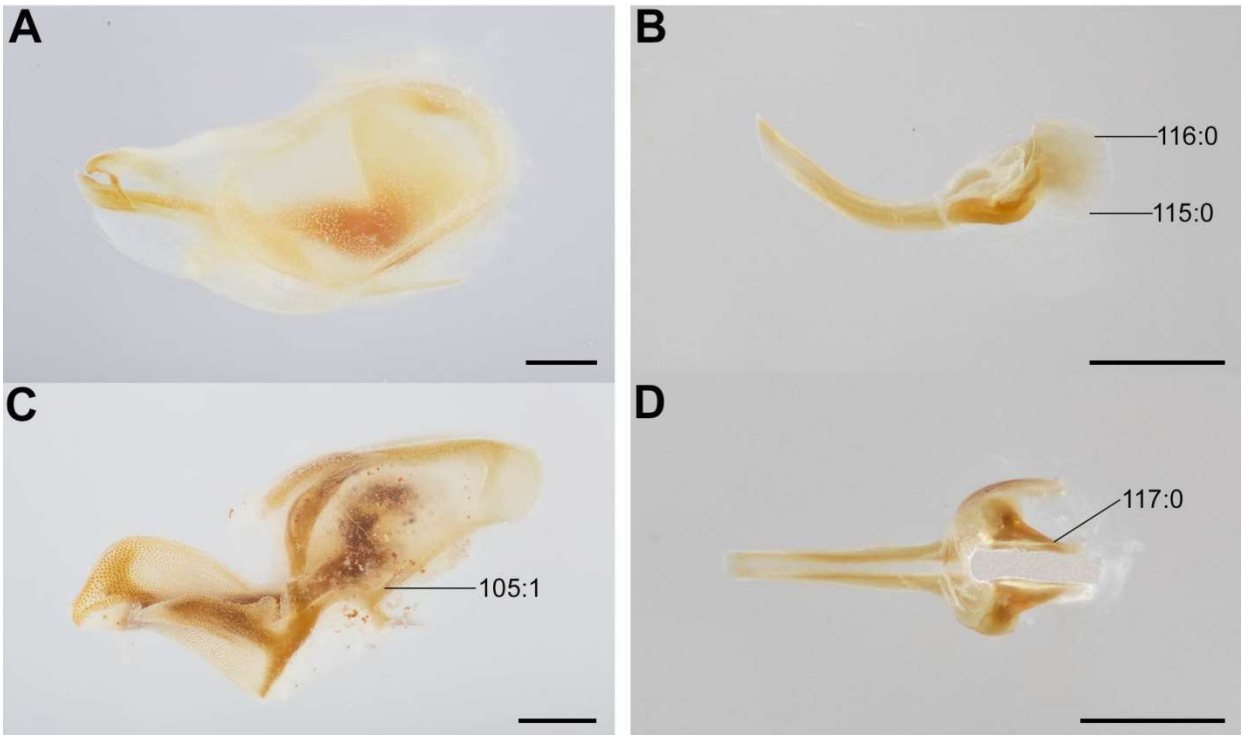

Figure 4.16. Ectophallus + Endophallus of some Pyrgomorphidae. A. *Acanthopyrgus finoti* (Madagascar), ecto+endophallus, lateral view; B. *Acropyrgus cadeti* (Madagascar), endophallus, lateral view; C. *Meubelia leytensis* (Philippines), ecto+endophallus, lateral view and D. *Acropyrgus cadeti* (Madagascar), endophallus dorsal view. Scale bar = 0.5 mm.

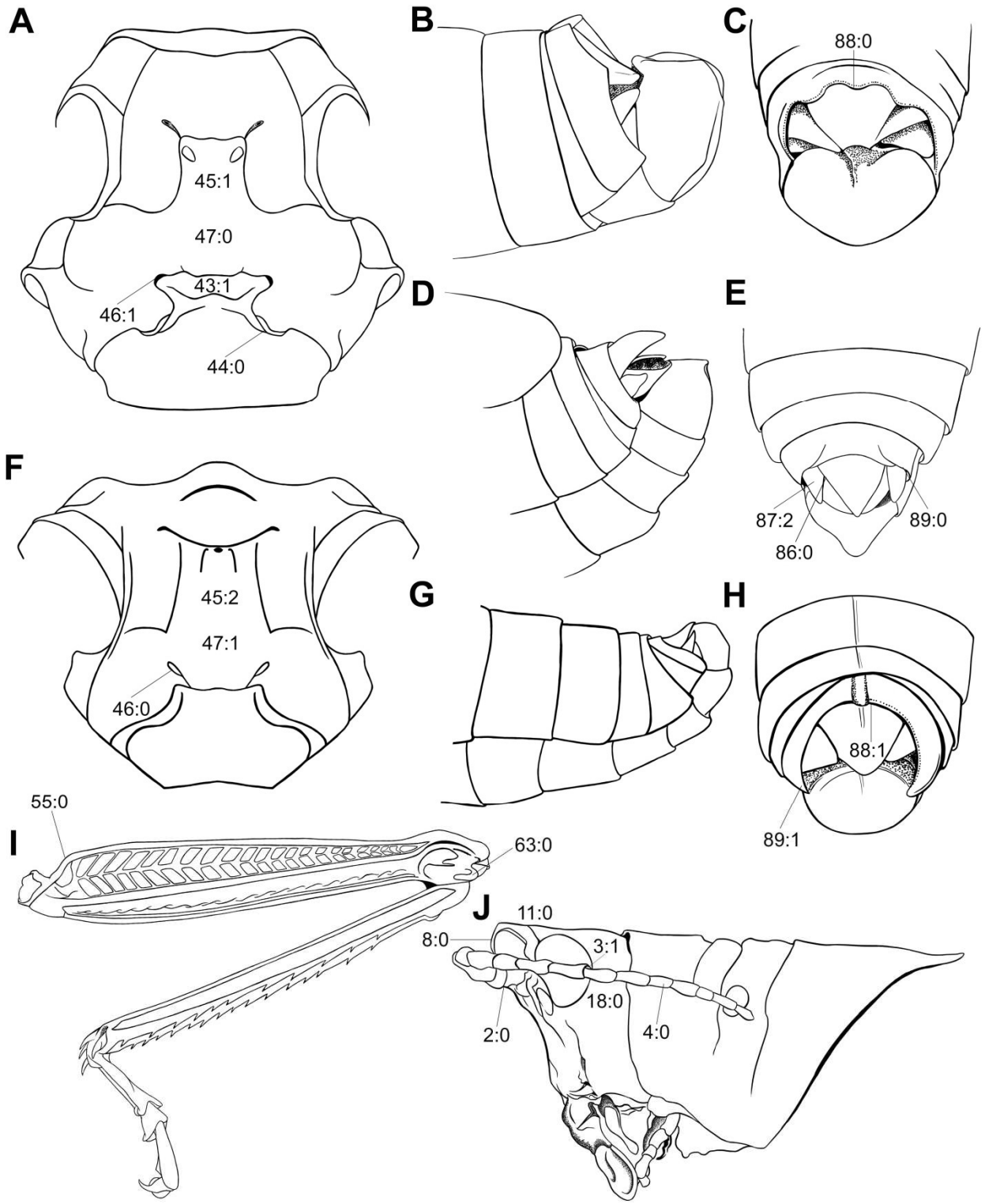

Figure 4.17. Illustrations of some Pyrgomorphidae 1. A. Meso and metathorax of *Poekilocerus pictus* (India), B & C. Lateral and dorsal view of tip of abdomen of *Chrotogonus oxypterus* (India); D & E Lateral and dorsal view of tip of abdomen of *Dictyophorus spumans* (South Africa); F. Meso and metathorax of *Sphenarium histrio* (Mexico); G & H. Lateral and dorsal view of tip of abdomen of *Sphenarium histrio* (Mexico); I. Left hind leg in lateral view of *Dictyophorus spumans* (South Africa) and J. Head and Thorax in lateral view of *Poekilocerus pictus* (India).

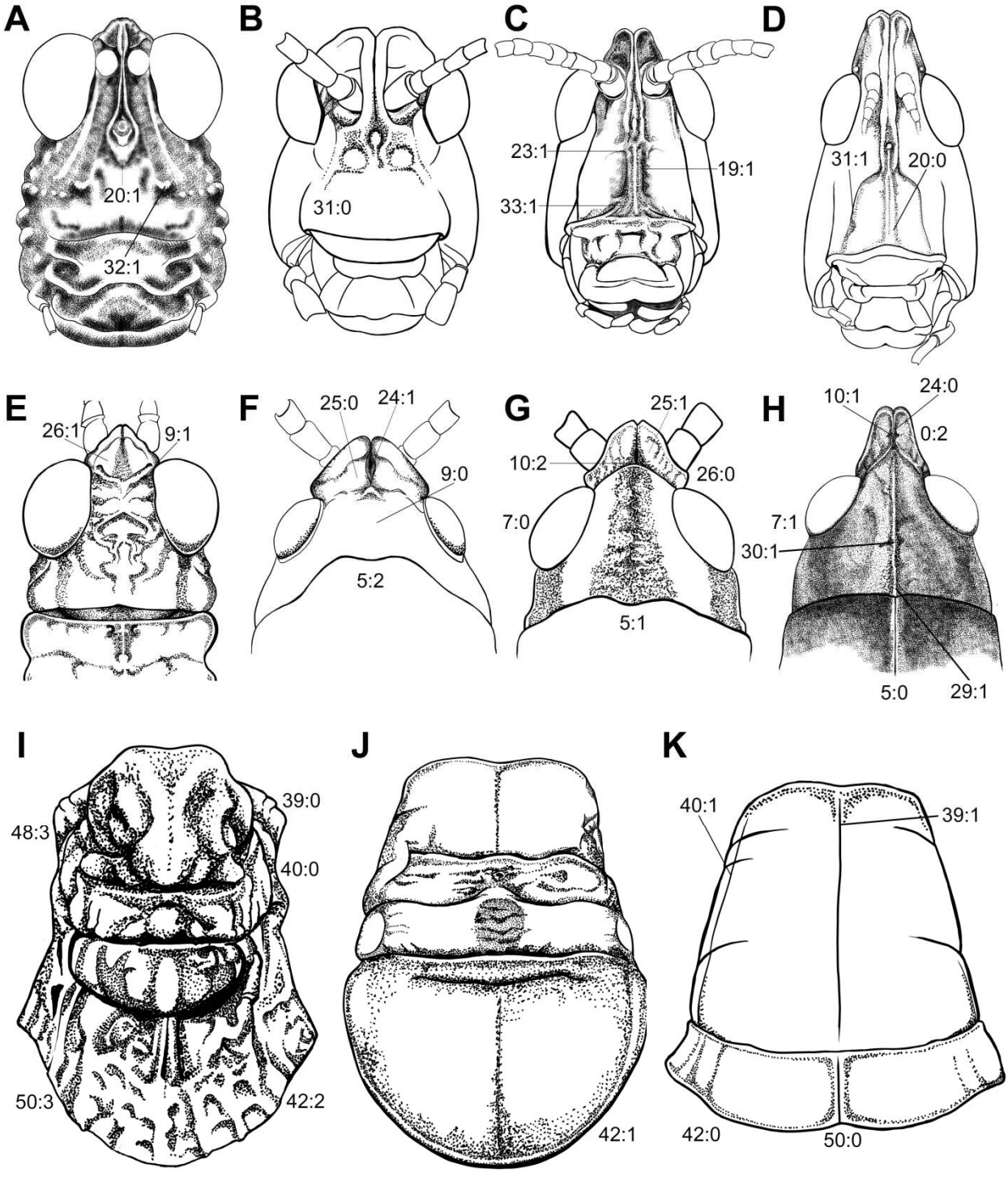

Figure 4.18. Illustrations of some Pyrgomorphidae 2. A-D. Heads in frontal view of *Chrotogonus oxypterus* (India), *Dictyophorus spumans* (South Africa), *Poekilocerus pictus* (India) and *Sphenarium histrio* (Mexico); E-H. Heads in dorsal view of *Chrotogonus oxypterus* (India), *Dictyophorus spumans* (South Africa), *Poekilocerus pictus* (India) and *Sphenarium histrio* (Mexico) and I-K. Pronotum on dorsal view of *Dictyophorus spumans* (South Africa), *Poekilocerus pictus* (India) and *Sphenarium histrio* (Mexico).

4.5 Discussion

4.5.1 Pyrgomorphidae is strongly monophyletic

The present study represents the first modern cladistic analysis of the family Pyrgomorphidae, which I strongly recover as a monophyletic group based on the following seven characters: the groove in the fastigium (0:2), the reduction of posterior projections in the epiphallus (94:0), the reduction of ancorae in the epiphallus (95:0), club-shaped oval sclerites (96:1), cingulum extending and reaching the ventral side enveloping endophallus (105:1), the medially situated endophallic apodeme (117:0), and the unconstricted ejaculatory and sperm sacs (118:0). While I now recognize this family as a distinct member of the superfamily Pyrgomorphoidea (Cigliano et al., 2017), there has been a tumultuous taxonomic history in determining its affinity within Caelifera.

Initially, Pyrgomorphidae was thought to be closely related to Pamphagidae because both families have the endophallic sclerites that are in ventral or medial position with respect to the spermatophore sac. Roberts (1941) described this arrangement as “Chasmosacci” and both Dirsh (1956) and Amédégnato (1976) suggested that the South African endemic family Lentulidae was also closely related to Pyrgomorphidae based on this genital arrangement. In his larger treatment of the classification of Acridomorpha, Dirsh (1975) elevated the “Chasmosacci” to a superfamily status and erected Pamphagoidea, which Otte (1994) followed for establishing the higher-level classification of Orthoptera. However, the placement of Pyrgomorphidae within Pamphagoidea was challenged when Flook and Rowell (1997) used partial mitochondrial ribosomal RNA genes of 32 caeliferan taxa to resolve the phylogeny of Caelifera. Their study included three pyrgomorphs (*Prosphena scudderi*, *Atractomorpha acutipennis,* and *Zonocerus elegans*), which

did not recover a sister relationship between Pyrgomorphidae and Pamphagidae. Instead, Pyrgomorphidae was found to be an early-diverging lineage within Acridomorpha, a group of grasshopper-like families within Caelifera. This new phylogenetic position was strongly supported when Flook et al. (2000) used additional loci from three genes (12S, 16S and 18S) to test the relationships, which led to the erection of a new superfamily, Pyrgomorphoidea, which included only the Pyrgomorphidae. Flook et al. (2000) added Lentulidae to the analysis, which was found to be more closely related to Pamphagidae, and quite divergent from Pyrgomorphidae. Eades (2000) used this finding and reinterpreted the homology of male phallic complex within Acridomorpha and hypothesized that Pyrgomorphoidea would be sister to Acridoidea (which includes both Pamphagidae and Lentulidae, as well as several other families). Indeed, the synapomorphies supporting Pyrgomophidae mostly are male genitalia characters, which suggests that the previous hypothesis of "Chasmosacci" was based on incorrect interpretation of genital homology.

More recently, additional molecular studies consistently found the sister relationship between Pyrgomorphoidea and Acridoidea (Hong et al., 2003; Leavitt et al., 2013; Lu & Huang, 2012; Song et al., 2015; Zhang et al., 2013). A recent divergence time estimate study of Orthoptera based on 9 fossil calibration points proposed that the origin of Pyrgomorphidae could be dated to the Cretaceous period (Song et al., 2015), suggesting that this family represents a much older lineage than other grasshopper families that it was originally associated with.

4.5.2 Phylogenetic relationships among major lineages within Pyrgomorphidae

This analysis finds that the subfamily Pyrgomorphinae is largely paraphyletic, but the subfamily Orthacridinae is monophyletic. This is not surprising given that the classification scheme established by Kevan and his colleagues (Kevan, 1976; Kevan & Akbar, 1964; Kevan et al., 1969, 1970, 1971, 1972, 1974, 1975) has not been stable. For example, Kevan concluded that there were not sufficiently distinctive features to divide the family into major subfamilies. Instead, they created two groups, ten series and 30 tribes. Some tribes were quite large while others comprised a few genera, and six were monogeneric. These divisions were made based on internal genitalia and some external morphological characteristics (Table 4.2). On the other hand, Dirsh (1975) divided Pyrgomorphidae into 13 subfamilies, based mostly on external characteristics, which largely, but incompletely overlapped with Kevan's tribes. Dirsh (1975) argued that grouping on the basis of internal genitalia was difficult because the diversity in the secondary structures in almost every genus. However, Dirsh's classification was largely ignored by most authors. Chinese authors have followed a different classification system, which was proposed by Yin (1982, 1984) who placed Pyrgomorphidae within Acridoidea and divided it into two families: Chrotogonidae, with four subfamilies (Taphronotinae, Chrotogoninae, Yunnanitinae and Mekongiellinae) and Pyrgormophidae, with two subfamilies (Pyrgormorphinae and Atractomorphinae). Later, Xia et al. (1994) added two subfamilies (Aularchinae and Tagastinae) to Chrotogonidae, but this classification scheme had never gain acceptance outside China. Xu et al. (2002) conducted a phylogenetic analysis based on 21 morphological characters and 10 representative pyrgomorph genera found in China, which did not find any support for the hypothesis of two families, but this finding did not lead to a revised classification in China.

The present study clearly divides Pyrgomorphidae into four main clades. Below, I discuss about each clade by describing synapomorphic characters as well their biology and biogeography, while contrasting with previous taxonomic work.

The clade A (figs 4.6E,F, 4.8C,D, 9, 4.10B-F) consists of the following tribes: Chapmanacridini (1 sp.), Geloiini (8 spp.), Gymnohippini (6 spp.), Ichthiacridini (10 spp.), Ichthyotettigini (7 spp.), Mitricephalini (6 spp.), Nereniini (26 spp.), Orthacridini (58 spp.), Popoviini (6 spp.), Sagittacridini (3 spp.), Psednurini (6 spp.), and Verduliini (13 spp). The members of this clade are typically small and have cylindrical body forms. In some cases, male cerci are enlarged and highly modified. In other cases, the posterior part of the abdomen is inflated. The wing reduction is widely present in the group. Based on this analysis, I have identified five characters uniting this clade: (i) quadrate pronotum (except *Colemania* and *Caprorhinus*) (34:0), (ii) posterior margin of pronotum in lateral view extending to the first coxae (except *Mitricephaloides*) (36:0), (iii) unconnected metasternal pits (except in *Meubelia* and Psednurini (46:0), (iv) the absence of tegmina (70:0), and (v) the absence of hind wings, except in *Mitricephaloides* (82:0). The clade A is essentially equivalent to the subfamily Orthacridinae, which is basically the group "A" of Kevan et al. (1969, 1970, 1971, 1972, 1974). I predict that the three tribes not sampled in this study, Brunniellini (Philippines), Fijipyrgini (Fiji), and Malagasphenini (Madagascar), are likely to be placed in this clade based on published descriptions of their morphology. The members of the clade A are distributed in both the New and Old World, but with a high level of endemicity. There are two endemic tribes to Mexico (Ichthyotettigini and Ichthiacridini), three endemic to Madagascar (Geloiini, Gymnohipini and Sagittacridini), and three endemic to Southeast Asia (Mitricephalini, Nereniini and Verduliini). The tribe Orthacridini is distributed in Africa and

Asia and consists of 56 species in 11 genera. The tribe Psednurini is the most strongly supported group within the clade A, with 10 synapomorphies. This tribe (6 spp. in 3 genera) is endemic to Australia and is associated to vegetation with stiff grasses, which the grasshoppers use their minute legs to grasp the circular stems (Rentz et al., 2003). The information about the biology and ecology of the tribes belong to clade A is very scarce. In studying Madagascar species, Braud et al. (2014) reported that *Gymnohippus marmoratus* lives in small salt-tolerant bushes in coastal dunes and that *Acanthopyrgus finoti* inhabits medium altitude forest in the highlands. Fontana et al. (2011) reported that the species of *Ichthyotettix* are found in partially stony to dry stony habitats with sparse bushes and very few herbs in Mexico. In general the Ichthyotettigini and Ichthiacridini are found in arid habitats in Mexico. Perhaps, the best-studied species in this clade is *Colemania sphenarioides*, which inhabits the Indian subcontinent and is a major pest on sorghum and wheat. It appears in large numbers approximately in cycles of 10-15 years. It has a mid-dorsal abdominal gland that secretes a milky fluid strong in odor that can reach up to 5 cm (COPR, 1982).

The clade B (Figs 4.7 and 4.8A,B) consists of the following tribes: Dictyophorini (11 spp.), Monistrini (15 spp.), Petasidini (2 spp.), Phymateini (22 spp.), Poekilocerini (4 spp.), and Taphronotini (9 spp.). This clade is united by four synapomorphies: a convex shape of the upper and lower marginal area of hind femur (58:1), thick carinae and carinulae in the hind femur (60:1), contrasting coloration in abdomen (93:1), and the presence of dorsal posterior processes of endophallic apodeme (116:1). The close relationships of some of the tribes included in the clade B have been previously proposed. For example, Kevan et al (1972) placed the tribes Poekilocerini and Phymateini in the Series VI. Kevan et al. (1974) further divided Tapronotini

into subtribes Aularchina and Taphonotina, and also suggested a close relationship between Taphronotini and Dictyophorini. Key (1985) suggested a relationship between the tribes Monistrini, Petasidini and Poekilocerini. This group is mainly distributed in Africa, Madagascar, Asia and Australia. The clade B includes some of the most familiar members of the family that are large and colorful. They commonly have well-developed and intricate pronotum with tubercles and spines. The tegmina are well developed although they are reduced in some cases. They exhibit aposematic coloration and feed on toxic plants, such as milkweeds (Whitman, 1990). The sequestration of secondary plant compounds as a chemical defense could be an important condition in this clade (Agrawal et al., 2012; Chapman et al., 1986; Euw et al., 1967; Modder, 1983). There is also evidence of detoxifying and neutralizing cyanogenic glycosides in some of these grasshoppers (Bessie & Agboola, 2013; Idowu et al., 2009). Some species have a mid-dorsal abdominal gland that can produce chemical defense, such as *Zonocerus*, *Phymateus* and *Poekilocerus* (Whitman, 1990). There is only other report of mid-dorsal abdominal gland outside this clade (*Colemania* in clade A). Others have different mechanisms of chemical defense such as openings in pronotum and abdomen (*Aularches* and *Taphronota*) for releasing toxic chemicals or production of toxic foams by combining hemolymph with air through spiracles (*Dictyophorus*) (Whitman, 1990). In Australia, *Petasida ephippigera* (fig. 4.3A) has a very strict diet in toxic shrubs and is not known to have any chemical release mechanism (Rentz et al., 2003). This bright orange and blue grasshopper is known as Leichhardt's Grasshopper in northern Australia and is culturally important as it is known in Aboriginal dreaming stories as Alyurr, children of the lightening man (Lowe, 1995). Several members of the clade B, including *Zonocerus*, *Phymateus*, *Taphronota,* and *Poekilocerus* are gregarious as nymphs in Africa and Asia (Whitman, 1990). The members of the Australian genus *Monistria* are found in different

habitats from coastal heaths to alpine woodlands and in some cases they are often abundant and can be destructive (Rentz et al., 2003).

The clade C (fig. 4.6A-D) consists of the genera *Rubellia*, *Mekongiella*, *Prosphena*, and *Sphenarium*, and is united by two synapomorphies, triangular cerci (87:2) and rectangular epiphallus (99:1). All of the genera included in this analysis are currently placed in the tribe Sphenariini (25 spp.), which suggests that the clade C is essentially Sphenariini. This tribe exhibits the most peculiar biogeographical patterns within the family. In this analysis, *Rubellia* is endemic to Madagascar, *Mekongiella* occurs in China, and *Prosphena* + *Sphenarium* occur in Central America. Kevan et al. (1972) further divided the tribe according to the geographic distributions into the subtribes: Rubellina (1 sp.) (Madagascar), Sphenexiina (2 spp.) (East Africa and Socotra), Mekongianina (10 spp.) (China), and Sphenariina (12 spp.) (Central America). I find that the pyrgomorph species occurring in the New World do not form a monophyletic group, but belong to other clades (A and B), which suggests that the New World has been colonized by ancestral pyrgomorphs from the Old World multiple times. The genus *Sphenarium* is culturally important in Mexico because it used as human food in the southern parts, but is considered a major pest species in the central Mexico. This genus consists of flightless, polyphagous, and univoltine species and has a wide altitudinal distribution (sea level to 2600 m.a.s.l.) (Sanabria-Urbán et al., 2015). For the Madagasacar endemic *Rubellia nigrosignata*, Braud et al. (2014) reported it from 5 to 1845 m.a.s.l. and it is categorized as a moderately important pest (regular but minor damage and not chemically treated), which affects shrubs and fruit trees and ocassionally rice. The Chinese Sphenariini are found up to 4800 m.a.s.l. (Kevan, 1966; Yin, 1984).

The clade D (Figs 4.4, 4.5A-D and 4.8E) consists of the following tribes: Atractomorphini (29 spp.), Chrotogonini (17 spp.), Omurini (4 spp.), Pseudomorphacridini (3 spp.), Pyrgomorphini (105 spp.), Schultessiini (2 spp.), and Tagastini (17 spp.). All these tribes are currently placed in the subfamily Pyrgomorphinae. This clade is characterized by the antennal base that is positioned in front of ocelli in lateral view (2:1), a row of tubercles between the eye and posterior border of head (18:1), a wider lower marginal area compared to upper marginal area (59:0), and the thick wing veins when functional tegmina are present (76:1). In general, the tribes belonging to the clade B have full tegminal, but of pale coloration. In some cases there are wing reductions. This clade is mostly distributed in the Old World with the exception of the representative of the tribe Omurini (*Omura*), which is found exclusively in South America. *Omura congrua* seems to prefer areas of high humidity (Kevan, 1977). The tribe Chrotogonini is the most robustly supported group within the clade B, with 16 synapomorphies, the presence of the collar of prosternum being the most evident character. Kevan et al. (1975) discussed that typical Chrotogonini and Pyrgomorphini (Series X) have similar phallic structures and that the members of Chrotogonini probably have a common origin with the Pyrgomorphini. Interestingly, Kevan et al. (1975) placed the genera *Pyrgomorpha*, *Anarchita,* and *Zarytes* in the same subtribe, Pyrgomorphina. It is important to point out that the tribe Pyrgomorphini is comprised of 105 species in 29 genera, which represents more than 20% of the species diversity in the family. Kevan et al. (1974) grouped the tribes Tagastini, Pseudomorphacridini, and Atractomorphini in the Series VIII. They suggested that the nearest relatives of Tagastini are Pseudomorphacridini, which is derived from Tagastini. They also suggested a probable affinity of these three tribes with Schulthessiini. It is necessary to include more genera to resolve the phylogenetic relationships of this tribe. The genus *Atractomorpha* is the best studied and preferred habitats associated with water and in

Australia can cause damage to some crops such as peanuts and tobacco and has the potential to attack cotton (Rentz et al., 2003). In India both nymphs and adults are important pests of tobacco and maize (COPR, 1982). The genus *Chrotogonus* can cause severe damage to cotton in Asia and cereals and coffee in Africa (COPR, 1982). The genus *Pyrgomorpha* attacks in Africa and Asia useful plants such as castor, cotton, cucumber, and wheat (COPR, 1982).

While most of the taxa included fall within the four clades discussed above, there are some groups that this analysis is not able to clarify their phylogenetic positions. I have included two genera (*Chlorizeina* and *Humpatella*) representing the tribe Chorizeinini (Fig 4.5E,F), but this tribe is not recovered as a monophyletic group. Both *Humpatella* and *Chlorizeina* share a constricted bridge of epiphallus with *Tagasta* (98:1) in the clade D. The genus *Chlorizeina* has the thick tegmina veins, which is only found in the clade D (76:1). However, both genera have the upper basal lobe of hind femora as long as the lower basal lobe (55:1), clearly pubescent hind tibiae (67:1), and a separation between the base of cerci and epiproct (86:1), which group them close to the clade A. Nevertheless, the longitudinal length of fastigium of vertex is shorter than the dorsal length of eye (7:0), which is a state widely present in the clades A, B, and D. The lateral carina of pronotum is absent (40:0) in *Humpatella* (as in the clades A and B) but is present (40:1) in *Chlorizeina* (as in the clade D). Finally, the posterior corners of last abdominal tergite are protruded (89:1) as in the great majority of the clade A, but this state is also present in some members of clade D. The inclusion of additional genera will help test the monophyly of the tribe and its position within Pyrgomorphidae. The tribe Desmopterini (Asia and Australia) includes 9 other genera apart from *Desmopterella*. Although *Desmopterella* (fig. 4.10A) is recovered as a sister group of the clade A because of the dorsoventral length of medial area of hind femur that is

wider when compared to upper and marginal area (57: 0), there are other characters that it has, such as the oval eyes (22:1) and foveolate texture of lateral pronotum (49:1), which are found both in the clades A and D. Interestingly the veins on tegmina are thin (76:0) (contrary to thick (76:1) in the clade D). However, the radial sector is poorly developed (77:0) such as in the members of the clade D and the first part of precostal area in tegmina is poorly developed (78:0) similar to the several members of the clade B and D. The general appearance of *Desmopterella* (form of pronotum, development of wings) as well as its distribution makes us think that its current position in the phylogeny may not be accurate. The inclusion of additional genera will help us to define the placement of this group in the family.

4.6 Conclusion and future directions

Pyrgomorphidae is a charismatic family that is evolutionarily intriguing, but any attempt to study this family has been impeded by the lack of a robust phylogeny. Although this taxon sampling is limited and there are additional character systems such as female genitalia that have not yet been included, this study represents the first explicit phylogenetic hypothesis of the family, which encompasses the spectrum of diversity for the group. This work provides an insightful phylogenetic basis for further testing monophyly of tribes and subtribes, and represents the first step toward building a natural classification for the family.

This family is an excellent model system for studying the evolution of warning coloration and chemical defense. The warning coloration, or the aposematic coloration, is a difficult characteristic to define and usually involves colors such as, yellow, orange, red, brown, black, white or combinations of these colors (Lev-Yadun, 2009), with the patterns being more

important than colors themselves (Dolenská et al., 2009). If I use the abdominal coloration as a proxy for aposematic coloration, I can infer that a contrasting pattern has evolved at least twice, in the clade B and in the genus *Colemania* of the clade A. However, this might not be an optimal way of characterizing aposematism because there are species that have bright contrasting patterns on head, thorax, and wings, but have uniformly colored abdomen such as the genus *Dictyophorus*. Furthermore, highly colorful members of *Parasphena* (clade D) and *Sphenarium* (clade C) (fig. 4.3C) are not known to be chemically defended. Therefore, it is clear that aposematism has many facets that require more careful investigations. Interestingly, some pyrgomorphs have a specialized mid-dorsal abdominal gland used for chemical defense that appears to be associated with the aposematic coloration. For example, all the four species in this analysis with a mid-dorsal abdominal gland (as *Zonocerus*, *Phymateus*, *Poekilocerus*, *Colemania*) possess aposematic coloration in the form of contrasting coloration in the abdomen (Figs 4.7C,D, 4.8A and 4.10F). However, the functional morphology and physiology of this gland is not well understood. Furthermore, there are other aposematic species that lack the gland, but use dorsal openings in the pronotum and abdominal spiracles to release toxic foam (Whitman, 1990). The variations of body coloration and the modes of chemical defense within Pyrgomorphidae make the family a unique system for future studies of aposematism.

The family also exhibits the diversity of wing forms from complete aptery to full macroptery that appeared to have repeatedly modified throughout the diversification, which provides an interesting comparative framework to study the evolution of wings. For example, I find that tegmina have been lost several times throughout the family with multiple regains in the clade A. However, this regain is usually in the form of microptery. Perhaps, there are possible

modifications in wing developmental pathways that allow this pattern, similar to the pattern found in walking sticks (Trueman et al., 2004; Whiting et al., 2003). In some cases, there are intraspecific wing length polymorphism, often within the same population, such as the genera *Monistria* (Rentz et al., 2003) and *Zonocerus* (Chapman et al., 1986), which may be used as a model system to study the evolution of wing development.

Based on the paraphyly and incongruence with previous data, this study clearly shows that much work is needed before proposing a new classification scheme. I consider that the addition of new evidence will allow us to refine diagnoses for groups at different levels in order to improve the taxonomy of Pyrgomorphidae. This work represents a beginning of studies that will include an increase in taxon sampling coupled with the inclusion of other sets of morphological characters as well as molecular data.

CHAPTER V

ON THE ORIGIN OF THE NEW WORLD PYRGOMORPHIDAE (INSECTA: ORTHOPTERA)

5.1 Introduction

Pyrgomorphidae (Orthoptera: Caelifera) are one of the most charismatic grasshopper families, well known for their vibrant body color and conspicuous sculpting patterns on pronotum, often featured in display collections of large and showy insects (Mariño-Pérez & Song, 2018). The family currently includes 487 valid species, most of which occur in the Old World, with a great majority (384 species) distributed in Africa and Asia. While some of the most colorful members of the family are familiar to the general public and well studied, the majority of pyrgomorphs are actually cryptic and less known. Among these insects, perhaps the least studied species are the obscure assemblages of pyrgomorphs that have diversified in the New World.

In the New World, there are only 41 species of Pyrgomorphidae (8.4% of total diversity in the family), representing 13 genera. They are currently classified in 4 tribes: Ichthiacridini, Ichthyotettigini, Omurini, and Sphenariini (Sphenariina) (Table 5.1). These tribes were established by Kevan et al. (1964) mostly based on male genitalia and external morphology, but their phylogenetic relationships amongst each other and to other lineages within Pyrgomorphidae are unclear. The New World Pyrgomorphidae (NWP) show very specific distribution patterns. Ichthiacridini (3 genera; 10 spp.) and Ichthyotettigini (4 genera; 7 species) are both endemic to Mexico, and Omurini (3 genera; 4 spp.) is found in the upper half of South America. The tribe Sphenariini includes four subtribes, of which only one subtribe (Sphenariina; 3 genera; 20 spp.)

Table 5.1. Synopsis of key features of New World Pyrgomorphidae.

Tribe	Ichthiacridini	Ichthyotettigini	Omurini	Sphenariini (Sphenariina)
Diversity	*Calamacris clendoni*, *Sphenacris crassicornis, Ichthiacris* (8 spp.).	*Sphenotettix nobilis, Pyrgotettix pueblensis, Piscacris* (2 spp.), *Ichthyotettix* (3 spp.)	*Algete brunneri, Omura congrua, Minorissa* (2 spp.).	*Prosphena scudderi, Sphenarium* (17 spp.), *Jaragua* (2 spp.)
General body form	Subfusiform to cylindrical	Cylindrical	Fusiform	Fusiform
Distribution	Mexico	Mexico	Upper half of South America	Mexico to Costa Rica and Dominican Republic
Habitat in general	Arid	Arid	Tropical	Arid to Tropical
Tegmina	Apterous and micropterous	Apterous	Apterous and macropterous	Apterous and micropterous

is found in the New World, distributed from Mexico to Costa Rica and Dominican Republic (Cigliano et al., 2018). The remaining three subtribes of Sphenariini are disjunctly distributed in Madagascar, East Africa, and China, respectively.

Morphologically, the NWP are characterized by their body forms that generally fall in two categories: fusiform, in which the head is conical, the pronotum expands towards metazona and the abdomen stretches towards its end. The second form is cylindrical, in which the body has the same width throughout the entire body (fig. 5.1). Regarding wings, there is a large variation from having fully functional wings (macropterous as in *Minorissa*) to very reduced non-functional wings (micropterous as in *Sphenarium*) and to complete loss of wings (apterous as in *Ichthyotettix*) (Mariño-Pérez & Song, 2018). Ecologically, the NWP occupy diverse niches from sea level up to 2,700 masl. They can be found in deciduous or semideciduous tropical forest, rainforest, cloud forest, pine forest, grasslands, xeric scrub and thorny scrub. They prefer open spaces with sunlight, usually found on the ground or perching on grasses, shrubs, trees and cacti. Of the NWP, the genus *Sphenarium* has been studied in depth in terms of their mating biology (Cueva del Castillo, 2003; Cueva del Castillo & Nuñez-Farfán, 1999), variation in size and color (Alves dos Santos, 2005; Sanabria-Urban et al., 2015; 2017), and phylogeographic patterns (Sanabria-Urban et al., 2015; 2017). For example, *Sphenarium* species show some of the longest mate guarding behavior in which males can spend up to 22 days (half of its adult life) after copulation mounted on the females (Cueva del Castillo, 2003; Cueva del Castillo & Nuñez-Farfán, 1999). In some areas in Mexico, *Sphenarium* species are agriculturally important pests of crops such as corn and beans (COPR, 1982), while in Oaxaca they have been used as food (known as chapulines) for centuries (Cerritos & Cano-Santana, 2008).

Figure 5.1. New World Pyrgomorphidae. **A.** *Ichthiacris rehni* Bolívar, 1905 female (Mexico). **B.** *Sphenacris crassicornis* Bolívar, 1884 male (Mexico). **C.** *Ichthyotettix mexicanus* (Saussure, 1859) couple (Mexico). **D.** *Pyrgotettix pueblensis* Kevan, Singh & Akbar, 1964 couple (Mexico). **E.** *Sphenotettix nobilis* Kevan, Singh & Akbar, 1964 couple (Mexico). **F.** *Jaragua oviedensis* Perez-Gelabert, Dominici & Hierro, 1995 female (Dominican Republic). **G.** *Jaragua oviedensis* Perez-Gelabert, Dominici & Hierro, 1995 male (Dominican Republic). **H.** *Prosphena scudderi* Bolívar, 1884 couple (Guatemala). **I.** *Sphenarium histrio* Gerstaecker, 1884 couple (Mexico). **J**. *Omura congrua* Walker, 1870 female (Colombia). Photo credits: A, B, E, H. Ricardo Mariño-Pérez. C, D. Paolo Fontana. F, G. Daniel Perez-Gelabert. H. Jiichiro Yoshimoto. J. Rob Westerduijin.

Because most pyrgomorphs are found in the Old World, the presence of these insects in the New World has drawn attention of several taxonomists. There have been three main biogeographical hypotheses proposed to explain the origin and diversification of the NWP (fig. 5.2). The first one was by Kevan and Akbar (1964) who hypothesized that the ancestral pyrgomorphs could have colonized the Americas at least twice from Asia. They based their hypothesis on the strong morphological resemblance (in body form and male internal genitalia) between the Chinese genera *Yunnanites* and *Mekongiana* (Sphenariini: Mekongianina) and the Mexican genus *Sphenarium* (Sphenariini: Sphenariina), and between the Asian members of the tribe Orthacridini and the Mexican tribes and Ichthiacridini and Ichthyotettigini. Kevan (1978) recognized that the family represents an ancient lineage and even invoked "Lemuria", a hypothetical and now discredited land bridge that was thought to exist in the Pacific to explain the distribution of pyrgomorphs in the Pacific islands. However, he thought that the NWP resulted from multiple colonization events from the ancient pyrgomorphs that originated from Asia, crossed the Bering land bridge to arrive in the New World and ultimately reach Central and South America. The second hypothesis was made by Amédégnato (1993) who considered Pyrgomorphidae to be closely related to the Old World grasshopper families, Pamphagidae and Lentulidae, as well as the South American endemic Tristiridae based on their male genitalia. She thought that Pyrgomorphidae originated in Asia and dispersed to Africa and some lineages colonized South America when the two continents were physically close. However, she did not specify how many times the colonization of South America could have taken place. The hypotheses of Kevan and Amédégnato have not been formally tested in a phylogenetic framework. The third hypothesis was proposed by Mariño-Pérez and Song (2018), who conducted the first modern cladistic analysis of Pyrgomorphidae based on morphology. They found that the NWP did not form a

monophyletic group based on a morphological phylogeny, suggesting that the New World has been colonized by ancestral pyrgomorphs from the Old World multiple times, but due to the scope of the paper, the exact origin in the Old World was not hypothesized. Unfortunately, none of the three biogeographical hypotheses has taken into account any time component.

In this study, I have investigated the biogeography of the NWP based on a molecular phylogeny generated using complete mitochondrial genomes and four nuclear genes. I have included representatives of all four tribes known from the New World, as well as a number of the Old World representatives of the family. I specifically test the three biogeographical hypotheses regarding the origin of the NWP, and infer a biogeographical scenario based on a divergent time estimate and a biogeographical analysis. I show that the current distribution of the NWP is a result of dynamic vicariance and dispersal events and propose a novel biogeographical hypothesis regarding the origin and diversification of the NWP.

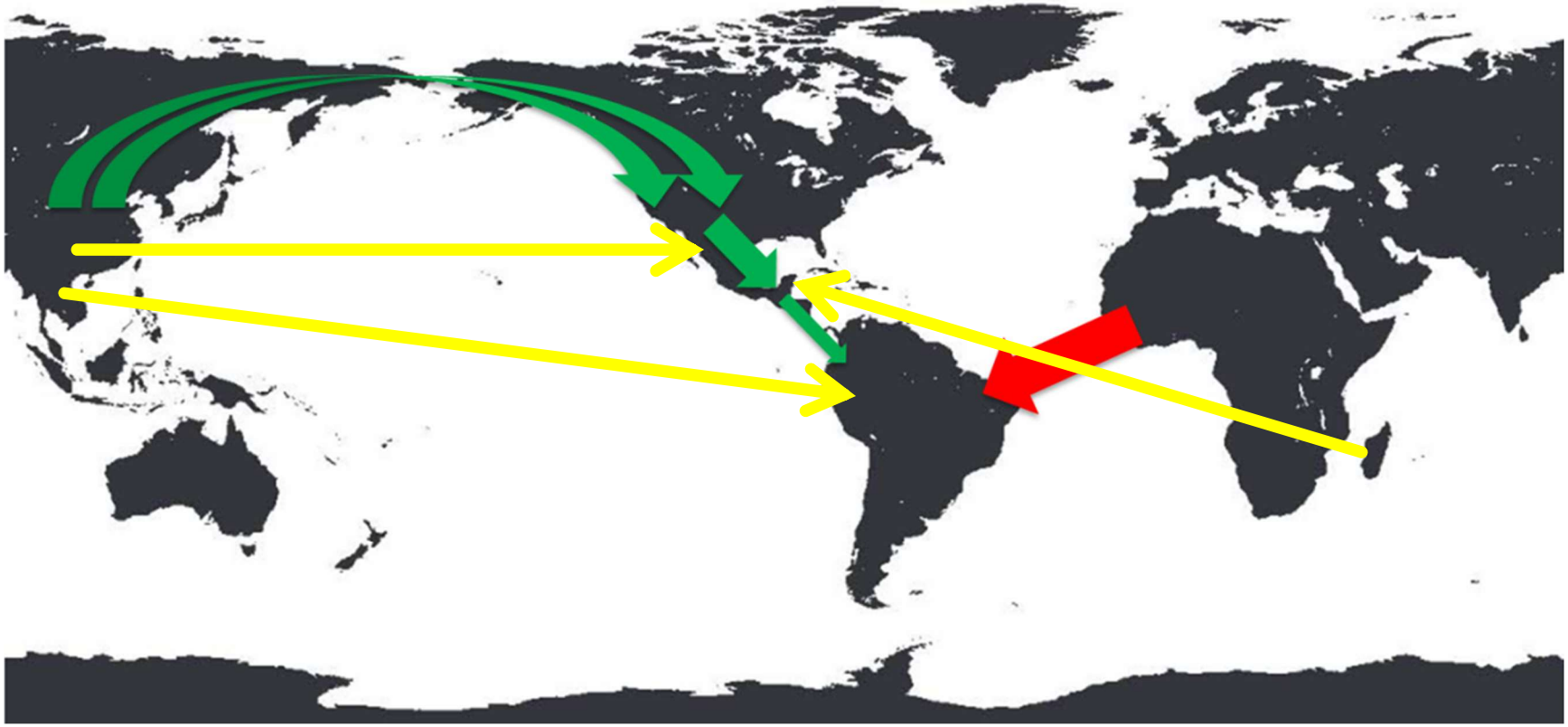

Figure 5.2. Biogeographical scenarios proposed to explain the origin and diversification of the New World Pyrgomorphidae. Kevan and Akbar (1964) hypothesized at least two colonization events from Asia through Bering land bridge (green arrows). Amédégnato (1993) hypothesized dispersal from Africa to South America (red arrow). Mariño-Pérez and Song (2018) implicitly suggested multiple origins from both Asia and Madagascar (yellow arrows).

5.2 Material and Methods

5.2.1 Taxon and character sampling

I sampled a total of 32 taxa, including 7 outgroup taxa representing 7 families of Acridomorpha (Acrididae, Lentulidae, Pyrgacrididae, Pamphagidae, Pneumoridae, Trigonopterygidae, and Tanaoceridae) and 25 ingroup taxa representing the family Pyrgomorphidae. Particularly, I included representatives of all four tribes present in the New World: Sphenariini, Ichthiacridini, Ichthyotettigini, and Omurini. For all terminals, I included partial or complete mitochondrial genome (mtgenome) data, 21 of which were newly sequenced for this study. The remaining mtgenomes were previously generated by us (Song et al., 2015) or obtained from GenBank (Table 5.2). I used *Tanaocerus koebelei* (Tanaoceridae) as a root. For nuclear genes, I generated complete 18S and 28S ribosomal RNA genes and Histone 3 (H3) gene for all except *Mekongiella*, *Mekongiana*, and *Yunannites* (due to lack of specimen). For *Atractomorpha*, I could not include H3 gene because it was not available, but obtained 18S and 28S from Genbank. For the 21 newly generated taxa I was also able to generate Histone H2B gene. DNA-grade tissue samples used for this study were collected by myself or provided by Hojun Song. They were preserved in 100% ethanol at -80°C freezer in the Insect Genomic Collection at Texas A&M University Insect Collection (TAMUIC-IGC). To generate mtgenome sequences for the 21 newly generated taxa, I performed shotgun sequencing of genomic DNA using the Illumina platform. To extract high molecular weight DNA required for Illumina sequencing, I used Gentra Puregene Tissue Kit (Qiagen) following the manufacture's guideline. The quality and concentration of DNA extracts were initially measured using either Qubit Fluorometer (Thermo Fisher) or DeNovix Spectrophotometer, and more thoroughly analyzed using Fragment Analyzer. I used Nextera XT DNA Library Prep Kit for library preparation and performed either

150bp paired-end (PE) sequencing using NextSeq500 or 125bp PE sequencing using HiSeq2500. Library preparation and next generation sequencing (NGS) were conducted at either Georgia Genomic Facility (NextSeq500) or Texas A&M Genomics and Bioinformatics Service (HiSeq2500). The resulting raw reads were quality-trimmed in CLC Genomics Workbench 8 (Qiagen). I used the MITObim pipeline to assemble mtgenomes *de novo* from the NGS reads (Hahn et al, 2013). All newly assembled mtgenomes were first uploaded as raw fasta files to MITOS (Bernt et al., 2013) to identify open reading frames (ORFs) and tRNAs. The initial MITOS annotation was used as a guideline to delimit gene boundaries and start and stop codons of each protein-coding gene was manually identified in Geneious 10.0.9 (Biomatters), following the recommendation by Cameron (2014). DNA sequence data generated for this study will be deposited to Genbank. I also extracted 18S, 28S, H3, and H2B genes from the shotgun sequence data by using 'Map to Reference' tool in Geneious. Using the pyrgomorph *Atractomorpha* sp. 18S and 28S sequences (KM853228 and KM853462), a pyrgomorph *Sphenarium totonacum* H3 sequence (KU147119) and a spider H2B sequence (XM_016058247) downloaded from GenBank as references, I used the Geneious mapper with low sensitivity to search for short reads that mapped to the reference sequences. This approach was very effective in extracting these four genes from the 21 newly generated taxa. The rest of nuclear genes used were obtained from a previous publication by Song et al. (2015) (Table 5.2).

Table 5.2. Taxonomic information and Genbank accession numbers for 7 outgroups and 25 ingroups. Blank spaces = To be uploaded.

Family	Subfamily	Tribe	Species	Voucher ID	mtgenome	18S	28S	H3	H2B
Outgroups									
Acrididae			*Locusta migratoria*	OR191	NC_001712	KM853191	KM853499	KM853674	
Lentulidae			*Lentula callani*	OR295	NC_020774	KM853234	KM853456	KM853632	
Pyrgacrididae			*Pyrgacris descampsi*	OR317	NC_020776	KM853246	KM853444	KM853620	
Pamphagidae			*Prionotropis hystrix*	OR151	JX913764	KM853180	KM853509	KM853684	
Pneumoridae			*Physemacris variolosa*	OR293	NC_014491	KM853233	KM853457	KM853633	
Trigonopterygidae			*Trigonopteryx hopei*	OR290	JX913767	KM853232	KM853458	KM856634	
Tanaoceridae			*Tanaocerus koebelei*	OR559	NC_020777	KM853342	KM853350	KM853526	
Ingroups									
Pyrgomorphidae	Orthacridinae	Psednurini	*Psedna nana*	OR528					
		Popoviini	*Colemania sphenarioides*	OR286		KM853230	KM853460	KM853636	
		Orthacridini	*Caprorhinus* sp.	OR562					
		Ichthiacridini	*Sphenacris crassicornis*	OR1334					
			Ichthiacris rehni	OR1333					
		Ichthyotettigini	*Pyrgotettix pueblensis*	OR1335					
			Sphenotettix nobilis	OR1336					
			Piscacris robertsi						
			Ichthyotettix mexicanus	OR1376					
	Pyrgomorphinae	Pyrgomorphini	*Tanita* sp.	OR283					
			Ochrophlegma sp.	OR279					

Table 5.2. Continued

Family	Subfamily	Tribe	Species	Voucher ID	mtgenome	18S	28S	H3	H2B
		Poekilocerini	*Poekilocerus bufonius*	OR152					
		Phymateini	*Phymateus morbillosus*	OR273		KM853223	KM853467	KM853642	
		Monistriini	*Monistria discrepans*	OR527		KM853332	KM853360	KM853536	
		Dictyophorini	*Dictyophorus spumans*	OR272					
		Desmopterini	*Desmoptera* sp.	OR278		KM853225	KM853465	KM853640	
		Chrotogonini	*Chrotogonus* sp.	OR284		KM853229	KM853461	KM853637	
		Omurini	*Algete brunneri*	OR281		KM853227	KM853463	KM853638	
		Sphenariini	*Sphenarium purpurascens*	OR1328					
			Prosphena scudderi	OR1337					
			Jaragua oviedensis	OR1338					
			Mekongiella kingdoni	GB	NC_023921				
			Mekongiana xiangchengensis	GB	NC_014450				
			Yunnanites coriacea	GB	JQ301463				
		Atractomorphini	*Atractomorpha sinensis*	GB	NC_011824				

5.2.2 Phylogenetic analyses

For mitochondrial and nuclear protein-coding genes, I aligned based on the conservation of reading frames by first translating into amino acids and aligning individually in MUSCLE (Edgar, 2004) using default parameters in Geneious. tRNAs were individually aligned in MUSCLE using default parameters, also in Geneious. 12S, 16S, 18S and 28S were aligned in MAFFT using the E-INS-i setting, also in Geneious. All these individual alignments were concatenated into a single matrix using SequenceMatrix (Vaidya et al., 2011). I divided the data into a total of 71 data blocks (13 mitochondrial and 2 nuclear protein-coding genes divided into individual codon positions, 22 tRNAs, 2 mitochondrial rRNAs, and 2 nuclear rRNAs). I then used PartitionFinder 2 (Lanfear et al., 2017) using the "greedy" algorithm (heuristic search) with branch lengths estimated as "unlinked" to search for the best-fit scheme as well as to estimate the model of nucleotide evolution for each partition.

I performed a maximum likelihood (ML) analysis and a Bayesian analysis on the total evidence dataset (21,853 aligned bp and 32 taxa). Because I included partial mtgenomes, our matrix included missing data for some taxa. Of the 32 taxa, 22 had more than 18,000 aligned bp. Five taxa had between 14,000 and 17,000 (*Caprorhinus*, *Colemania*, *Ichthyotettix*, *Mekongiana* and *Mekongiella*) and two taxa had around 11,000 bp (*Desmoptera* and *Ichthiacris*). Only three had a significant amount of missing data (*Jaragua* 9,726 bp; *Pyrgotettix* 6,579 bp and *Yunnanites* 5,113 bp). For the ML analysis, I used the best-fit partitioning scheme (17 partitions) recommended by PartitionFinder with the GTRCAT model applied to each partition and analyzed using RAxML 7.2.8 (Stamatakis et al., 2008) on XSEDE (Extreme Science and Engineering Discovery Environment, https://www.xsede.org) through CIPRES Science Gateway (Miller et al., 2011). Nodal support was evaluated using 1,000 replications of rapid bootstrapping

implemented in RAxML. For the Bayesian analysis, I used default priors and applied a different, unlinked model for each partition, as recommended by PartitionFinder, and ran four runs with four chains each for 100 million generations, sampling every 2,500 generations in MrBayes 3.2.6100 (Ronquist et al., 2012). I plotted the likelihood trace for each run to assess convergence in Tracer (REF), and discarded an average of 25% of each run as burn-in. This analysis was also run on XSEDE through the CIPRES Science Gateway. For both ML and Bayesian analyses, the resulting trees were visualized in Geneious.

5.2.3 Divergence time estimation

In order to estimate timing and rates of divergence in the family Pyrgomorphidae, I performed a divergence time estimate analysis using BEAST v.1.8 (Drummond et al., 2012). There is only one fossil pyrgomorph known. Kevan (1965) reviewed a fossil from Miocene (originally described as an Oedipodinae (Acrididae)), but placed it as Pyrgomorphidae (*Miopyrgomorpha fischeri*). The estimated age of this fossil (11.6 to 5.3 mya) is very recent and thus it is not useful for calibrating the age of the group, which Song et al. (2015) estimated to be the early Cretaceous. Therefore, I decided to use two estimates that Song et al. (2015) calculated by using nine fossil calibration points. The first calibration point was 152.79 mya, which was estimated for the clade that united Pneumoroidea, Trigonopterygoidea, Pyrgomorphoidea, and Acridoidea. The second calibration point was 140.43 mya for the clade consisting of Pyrgomorphoidea and Acridoidea. For this analysis, I used the best-fit partitioning scheme and the models of nucleotide evolution recommended by PartitionFinder. I created an xml file in BEAUti (Drummond et al., 2012), specifying the starting tree, fossil priors, monophyly constraints, and parameters for

molecular clock models. I used the relaxed clock log normal model for the clock model, the birth-death model with a uniform distribution as a tree prior, and a log normal distribution as a distribution prior for calibration points. To assess convergence across independent runs, I conducted ten separate analyses each for 100 million generations, sampling every 2,500 generations. I inspected the results using Tracer (Rambaut and Drummond, 2003–2009) and discarded 25% of each run as burn-in, and combined the two best trees that converged using LogCombiner (Rambaut and Drummond, 2002–2013a). A maximum clade credibility tree was summarized in TreeAnnotator (Rambaut and Drummond, 2002– 2013b), and visualized in FigTree.

5.2.4 Ancestral range estimation

I used the R package BioGeoBEARS [Biogeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts] (Matzke, 2013) in R (R Core Team, 2017) to infer the biogeographical history of the New World Pyrgomorphidae. BioGeoBEARS performs different models of ancestral range estimation because different ancestral-area reconstructions have different assumptions and are likely to produce conflicting outputs. The input files were: (1) a phylogeny, and (2) a file of geographical ranges indicating presence/absence of each species in each discrete area in the analysis. I compared six models implemented in the program: (1) DEC (dispersal-extinction-cladogenesis) (Ree et al., 2005); (2) DEC+J (including founder-event speciation); (3) DIVALIKE, a likelihood version of DIVA (dispersal-vicariance) (Ronquist, 1997); (4) DIVALIKE+J (including founder-event speciation); (5) BAYAREALIKE, a likelihood version of the Bayesian inference of historical biogeography for discrete areas

(BayArea; Landis et al., 2013); and, (6) BAYAREALIKE+J (including founder-event speciation). The six models included two free parameters (*d* = dispersal and *e* = extinction). I defined nine areas; North America (from USA to Panama), Caribbean, South America, Africa (Sub-Saharan) including Madagascar, West Palearctic (Europe and Northern Africa), India, Template Asia (China), Tropical Asia and Australia. Likelihood values of these models were compared using Likelihood Ratio Test. I used Akaike Information Criterion (AIC) to directly compare how well the different models fit the data and to select the most likely biogeographical scenario (Matzke, 2013, 2014).

5.3 Results

5.3.1 Phylogeny of Pyrgomorphidae and the position of the New World genera

I recovered monophyletic Pyrgomorphidae with strong nodal support in both ML and Bayesian analyses (figs. 5.3 and 5.4). The tree tropology was highly congruent between the two analyses and only three taxa with low support value in the ML analysis (*Atractomorpha*, *Mekongiella* and *Chrotogonus*) were incongruent in both topologies but their placements did not affect our discussion and conclusion about the origin of the NWP. The NWP did not form a monophyletic group, but instead resulted in three separate clades spread throughout Pyrgomorphidae (figs 5.3 and 5.4): (i) The clade comprised of the South American *Algete* (Omurini) and the Caribbean *Jaragua* (Sphenariini: Sphenariina) that diverged earlier than other NWP clades; (ii) The clade comprised of the Mexico and Central American *Sphenarium* and *Prosphena* (Sphenariini: Sphenariina), recovered as sister to the African *Ochrophlegma* and *Tanita* (Pyrgomorphini: Pyrgomorphina); and (iii) The clade comprised of the Mexican tribes Ichthiacridini (*Sphenacris*

and *Ichthiacris*) and Ichthyotettigini (*Pyrgotettix*, *Sphenotettix*, *Piscacris* and *Ichthyotettix*). In terms of four tribes that include the NWP, I found that Ichthiacridini and Ichthyotettigini were monophyletic, but Sphenariini (Sphenariina) was paraphyletic because *Jaragua* grouped with *Algete*, rather than *Sphenarium* and *Prosphena.* Because I only included one representative of Omurini (*Algete*), I could not test the monophyly of this tribe.

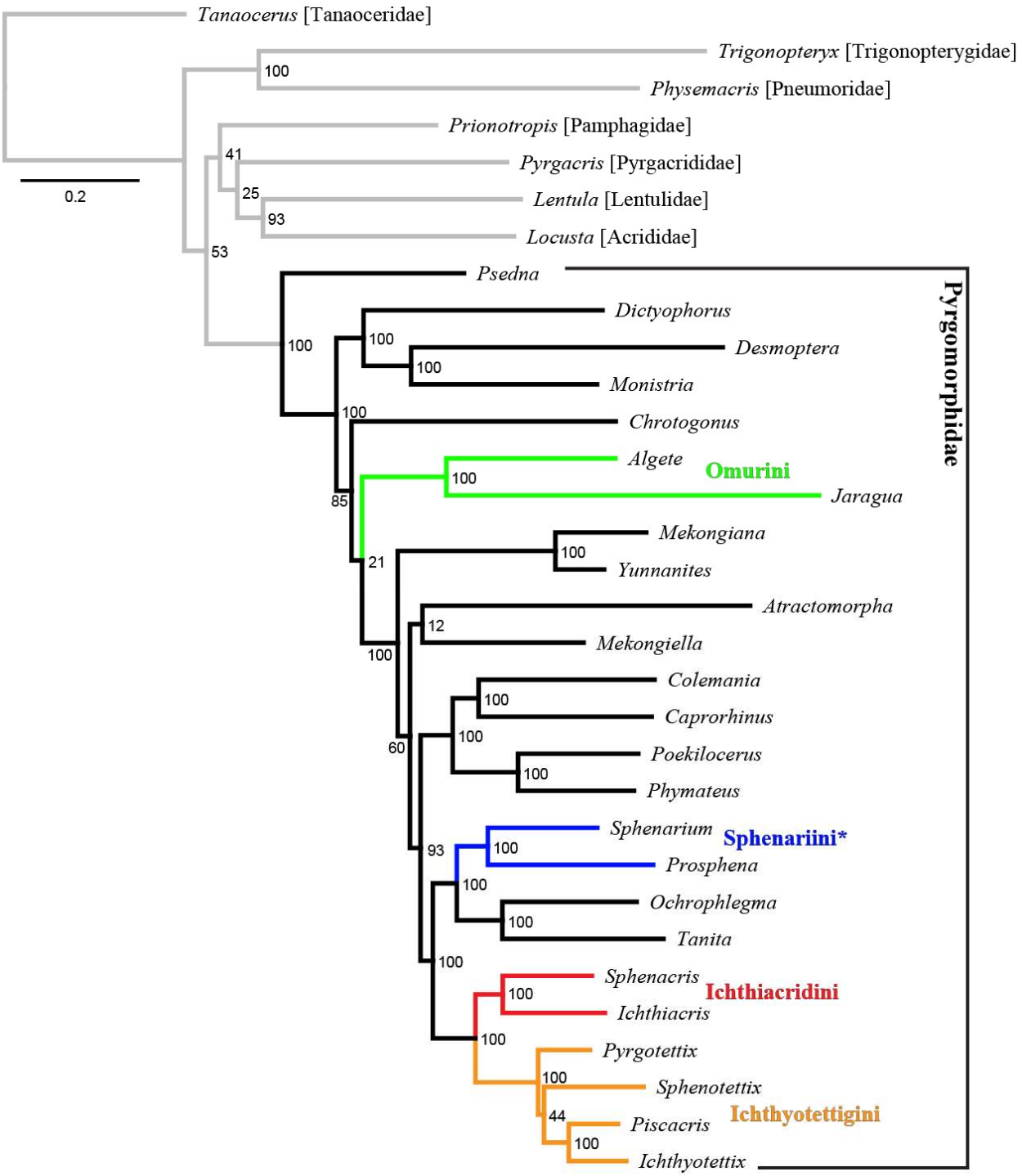

Figure 5.3. Phylogeny of Pyrgomorphidae based on RAxML analysis. The numbers on nodes are bootstrap support values.

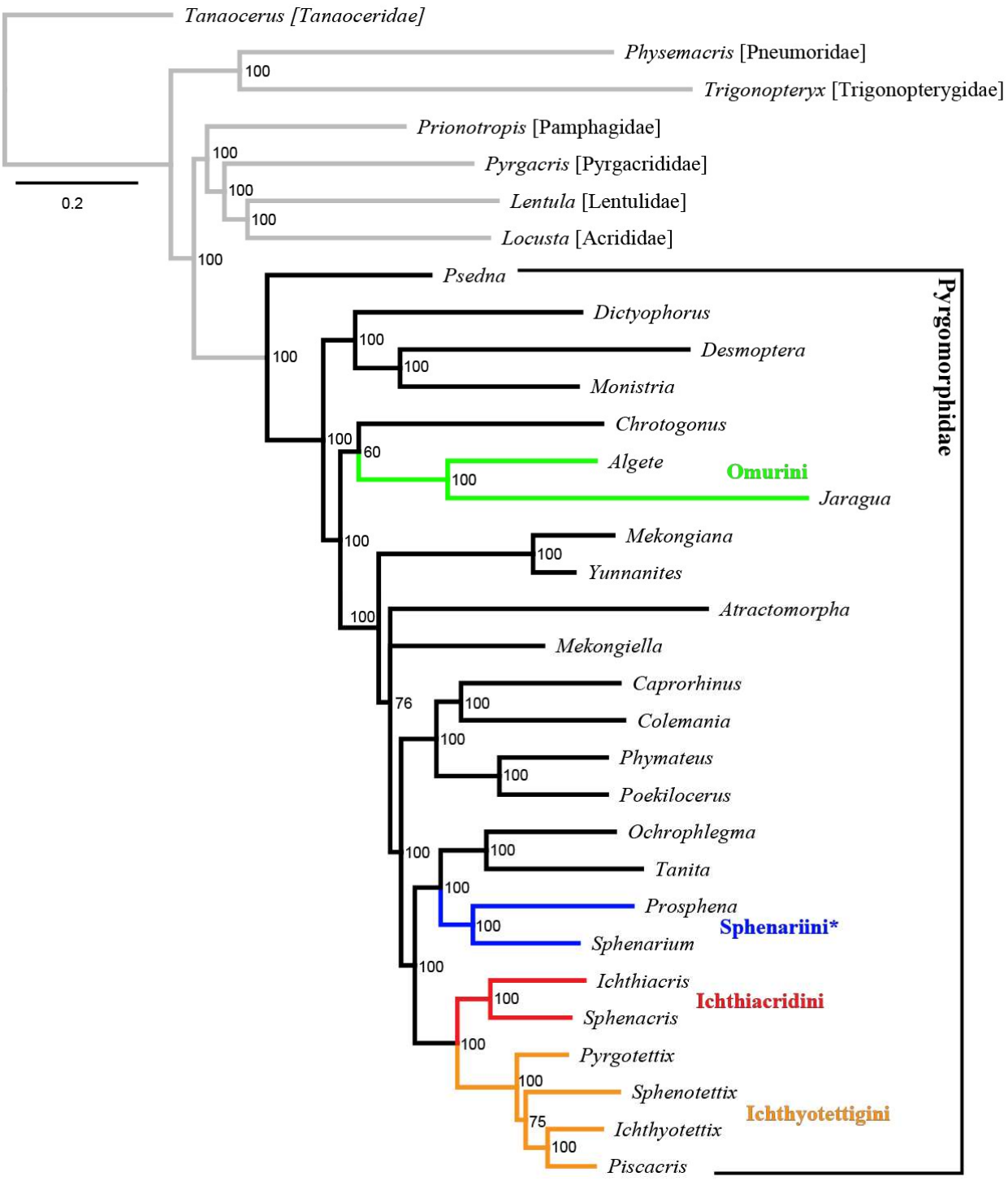

Figure 5.4. Phylogeny of Pyrgomorphidae based on Bayesian analysis. The numbers on nodes are posterior probability values.

5.3.2 Divergence time estimate and biogeographical history of the New World Pyrgomorphidae

Our divergence time estimate analysis suggested that Pyrgomorphidae diverged from other grasshopper families about 121 mya ± 18 mya (Early Cretaceous) and the tribal-level diversification took place until the Cenozoic (fig. 5.5). Our BioGeoBEARS analysis recommended DIVALIKE + J (LnL=-89.09) as the best-fit model (Table 5.3 and fig. 5.6). The origin of Pyrgomorphidae is estimated to be somewhere in an area comprised of Australia, Africa, India and Tropical Asia. I inferred that there were two independent events that resulted in the NWP. The first event could be a colonization from Africa to Northern South America or a vicariance event and occurred about 96 mya in the beginning of the Late Cretaceous (Cenomanian) from Temperate Asia to Africa and then South America. Taking the confidence interval into account, this event could have taken place either when the distance between Africa and South America was narrow (inferring dispersal) or when both landmasses were still together (inferring vicariance). This resulted in the clade consisting of *Algete* and *Jaragua*, which represents the earliest lineage of Pyrgomorphidae to colonize and diversify in the New World. The second colonization occurred towards the end of the Late Cretaceous (Maastrichtian) from Africa to South America and then North America. I inferred that the common ancestor of Ichthiacridini, Ichthyotettigini, *Sphenarium* + *Prosphena*, and *Ochrophlegma* + *Tanita* colonized across the Atlantic Ocean. This clade diverged into two lineages around the Cretaceous–Paleogene (K–Pg) boundary, one that gave rise to Ichthiacridini and Ichthyotettigini, another to the rest. It is also possible to infer that the common ancestor of *Ochrophlegma* and *Tanita* (Pyrgomorphini: Pyrgomorphina) recolonized Africa via eastward transatlantic route around 59 mya (Paleocene). Equally parsimonious explanation is two colonization events from Africa.

Table 5.3. The results of BioGeoBEARS analysis.

Model	LnL	numparams	d	e	j	AIC	AIC_wt
DEC	-99.6736	2	0.00091	0.001982775	0	203.8	5.00E-05
DEC+J	-89.4102	3	0.000538	1.00E-12	0.038367	185.7	0.42
DIVALIKE	-101.049	2	0.00098	0.000712037	0	206.5	1.30E-05
DIVALIKE+J	-89.0915	3	0.000588	1.00E-12	0.034504	185	0.58
BAYAREALIKE	-100.946	2	0.000551	0.010518348	0	206.3	1.40E-05
BAYAREALIKE+J	-95.8684	3	0.000298	0.007218214	0.014231	198.6	0.0007

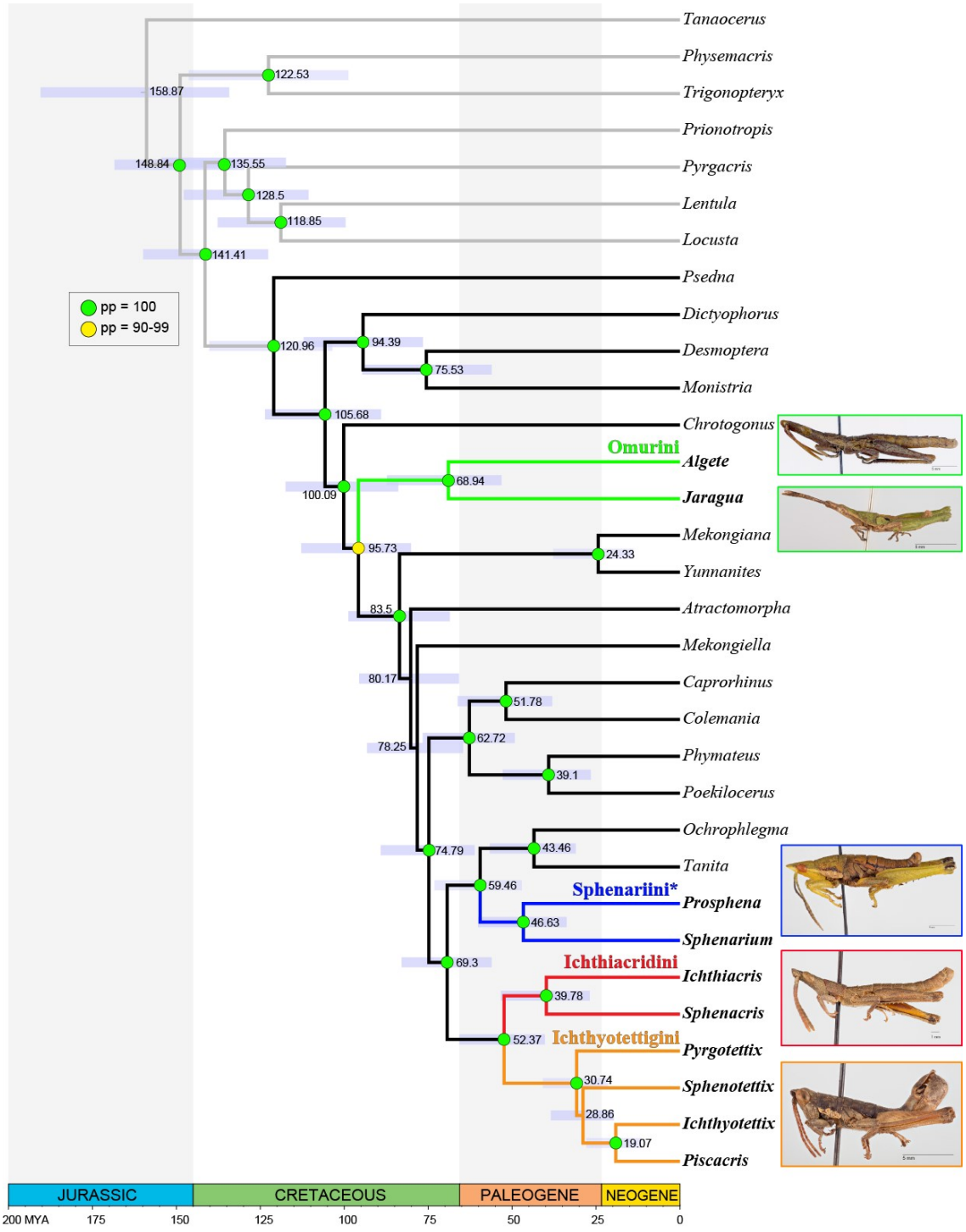

Figure 5.5. Dated phylogeny of Pyrgomorphidae based on BEAST analysis. The numbers next to nodes are estimated divergence time in million years. The light blue bars on nodes represent 95% confidence interval. Green and yellow dots on nodes represent 100% and 90-99% posterior probability values, respectively. The posterior probability values below 90 are not shown.

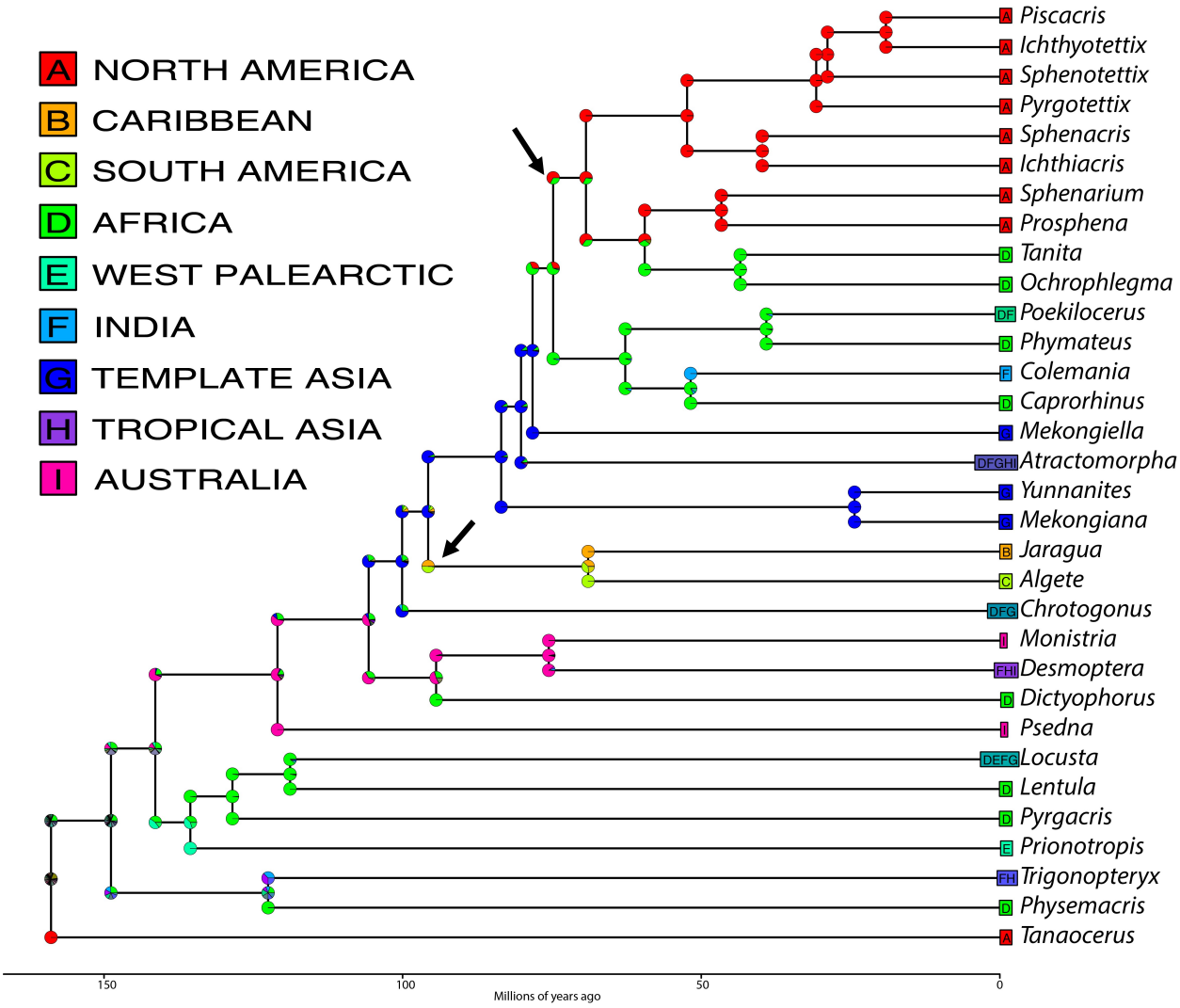

Figure 5.6. The result from the BioGeoBEARS analysis under DIVALIKE+J model (d=6e-04; e=0; j=0.0345; LnL=-89.09). The colored circles on the nodes represent the probabilities of each possible geographical range just before and after each speciation event. Some of the colored circles do not match with one of the pre-defined colors for the regions, which show ambiguity in the ancestral distribution. Arrows indicated the two NWP lineages.

5.4 Discussion

5.4.1 Phylogeny of Pyrgomorphidae and the placement of the New World genera

This study represents the first formal test of the monophyly of New World Pyrgomorphidae based on molecular data. Previous molecular studies included some members of Pyrgomorphidae as part of their taxon sampling, but did not specifically set out to understand the internal relationships of this family. For example, Flook and Rowell (1997) included three Pyrgomorphidae taxa (*Prosphena scudderi*, *Atractomorpha acutipennis* and *Zonocerus elegans*), Flook et al. (1999, 2000) included *Prosphena scudderi* and *Pyrgomorpha conica*, and Hong et al. (2003) used *Mekongiella kingdoni*, *Atractomorpha acutipennis* and *A. sinensis*. Zhang et al. (2013) and Leavitt et al. (2013) used *Atractomorpha sinensis*, *Mekongiella xizangensis* and *Mekongiana xiangchengensis*. In these six studies, the taxon sampling was low (2-3) and did not allow to infer internal relationships for Pyrgomorphidae. Lu and Huang (2012) used COI gene of *Mekongiana xiangchengensis*, *Yunnanites coriacea*, *Mekongiella xizangensis,* and *Atractomorpha sinensis* but found it to be paraphyletic because the only representative of Pneumoridae (*Physemacris variolosa*) appeared inside the Pyrgomorphidae. Song et al. (2015) inferring the phylogeny of Orthoptera using 258 taxa included eleven Pyrgomorphidae taxa and recovered monophyly as well as two clades that I have recovered in the present study, *Colemania* + *Phymateus* and *Monistria* + *Desmoptera*. The strength of the present study is the inclusion of 25 Pyrgomorphidae taxa, which is by far the largest molecular phylogenetic analysis focusing on this family, with an emphasis in the NWP (10 out of 13 genera) with 12 non-NWP and 7 outgroups (figs. 5.3 and 5.4).

Recently, Mariño-Pérez and Song (2018) proposed a morphological phylogeny of Pyrgomorphidae based on 119 characters, covering 28 out of 31 current recognized tribes, and found the family to be monophyletic, but only Orthacridinae, one of two subfamilies, was recovered as monophyletic. The other subfamily, Pyrgomorphinae, was recovered as a paraphyletic grade. The present study is narrower in scope compared to this previous study because the aim here is to specifically test the origin of the NWP. As such, my current taxon sampling includes only 15 tribes, representing less than 50% of tribal-level diversity. Thus, it is difficult to compare the present results based on molecular data directly with my previous work based on morphology, but I did find some notable discrepancies between the two. For instance, in the morphological study, I included four sphenariine genera (*Rubellia*, *Mekongiella*, *Prosphena*, and *Sphenarium*) and recovered the tribe Sphenariini as monophyletic (as the clade C in Mariño-Pérez and Song 2018). In this study, I did recover a sister relationship between *Prosphena* and *Sphenarium*, but *Mekongiella* did not cluster with the two former genera, thus making Sphenariini polyphyletic. A second clade recovered in the morphological analysis was the clade B which comprised among others the genera *Monistria, Dictyophorus, Phymateus,* and *Poekilocerus*. However, in this study, these genera did not form a monophyletic group, but scattered throughout the phylogeny. This type of incongruence in topologies between morphological and molecular phylogenies is often reported in literature, but what is surprising in this particular case is how dissimilar the higher-level relationships are. This disparity can be largely attributable to the fact that Pyrgomorphidae is old (139-104 mya) and that morphological convergence is rampant in this lineage. This family currently has less than 500 extant species, but given the diversity of biology and morphology, it is conceivable that it could have contained many more species in the past. Throughout the long period since the divergence, a number of

lineages that were intermediate between today's highly divergent lineages could have gone extinct, leaving numerous morphologically disparate groups. In fact, the reason Kevan created so many tribes was because he could not find any intermediate lineages (Kevan et al. 1969). Morphological convergence is a well-known phenomenon in grasshoppers, as Uvarov (1966) specifically discussed about ecomorph convergence. In Pyrgomorphidae, it appears that similar selective pressures have led to a lot of morphological convergence among divergence lineages, even in male genitalia, which has played a crucial role in creating confusion when coding morphological characters. For example, fusiform body has clearly evolved multiple times, and some of the morphological convergence is so convincing that my previous character coding could have been affected by them.

Having said, that, however, there are some similarities between the two analyses as well. For instance, both analyses recovered the relationship between *Sphenarium* and *Prosphena,* and *Poekilocerus* and *Phymateus*. This suggests that at finer scales (such as between two closely related genera), morphological characters show congruent patterns with molecular data. I need to consider a careful inspection of homology statements in a taxon-expanded phylogeny based on morphology from the insights generated from this molecular evidence. This will lead to a better understanding of the evolution of this interesting family.

Our analysis did not find the NWP as a monophyletic group, but rather as consisting of three separate clades, spread throughout the phylogeny of Pyrgomorphidae (figs. 5.3 and 5.4). Mariño-Pérez and Song (2018) also recovered a similar pattern in that the New World genera included in their study (*Omura*, *Prosphena*, *Sphenarium*, *Ichthyotettix*, and *Sphenacris*) did not form a monophyletic group. In this study, the first clade of the NWP consists of the Caribbean genus *Jaragua* and the South American genus *Algete* (green in figs. 5.3 and 5.4). Currently, *Jaragua* is

classified as a member of the tribe Sphenariini (Sphenariina) and *Algete* is classified under Omurini. *Jaragua* is the only pyrgomorph known from the Caribbean, endemic to Dominican Republic, and described in 1995. When the genus was described, it was placed in Sphenariini because of the resemblance in general shape of the epiphallus of *Jaragua* with that of the Chinese genus *Mekongiella* (Sphenariini: Mekongianina), and because of the intraspecific color variation patterns that are similar to *Sphenarium* (Sphenariini: Sphenariina), it is possible to find various color morphs in a single population (Sanabria-Urbán et al. 2015). However, Perez-Gelabert et al. (1995) discussed that the relationship to the Mexican and Central American genera *Sphenarium* and *Prosphena* was not clear based on general morphology. They commented that there were multiple morphological differences compared to *Sphenarium* and *Prosphena* such as size, pronotum form and fastigium of vertex length, and proposed that *Jaragua* would be a relictual form that has changed little due to isolation. The size of adults (the smallest of all known NWP) was attributed to their island habitat (Losos and Ricklefs, 2009). They also discussed that the most distinct morphological character of *Jaragua* is a triangular projection of the lateral pronotal lobes, which is seen only in the South American genus *Minorissa*, which belongs to Omurini, but they did not place the genus within Omurini because they considered genitalia resemblance with Asian Sphenariini was enough to group it there. I did not use *Minorissa* in this analysis, but did include another South American omurine genus, *Algete* that does not have the lateral pronotal lobe but share other characteristics such as the length of fastigium and the form of hind femur. Our phylogeny suggests that *Jaragua* is more closely related to Omurini, than to Sphenariini, and thus future work is needed to reassign *Jaragua* to Omurini.

The second NWP clade is composed of the Mexican and Central American genera *Sphenarium* and *Prosphena* (blue in figs. 5.3 and 5.4). These two genera are assigned to the subtribe Sphenariina of the tribe Sphenariini, which includes four subtribes that have disjunct distribution patterns. Kevan and Akbar (1964) created these subtribes to unite eight genera that are morphologically similar: Sphenariina to include *Sphenarium* and *Prosphena*, Rubelliina to include a Madagascar genus *Rubellia*, Sphenexiina to include two East African genera *Sphenexia* and *Xenephias*, and Mekongianina to include three Chinese genera *Mekongiana*, *Mekongiella* and *Yunnanites*. As mentioned above, *Jaragua* was later added to Sphenariina (Perez-Gelabert et al. 1995). In our previous phylogeny based on morphology, I included *Rubellia*, *Mekongiella*, *Prosphena*, and *Sphenarium*, and found them to form a monophyletic group (Mariño-Pérez and Song 2018). However, this clade was supported by only two homoplasious characters: triangular male cerci and rectangular epiphallus. In the present phylogeny, the monophyly of Sphenariini is not supported. Moreover, I found the subtribes Sphenariina and Mekongianina to be paraphyletic and recover in different clades. I did not include representatives from Rubelliina and Sphenexiina, but it is clear from our topology that the molecular data do not agree with the morphology. This pattern suggests that Sphenariini is possibly an artificial group at best, defined by convergent morphological traits with monophyletic relationships only in closely geographic taxa such as *Sphenarium* and *Prosphena* in Central America and *Mekongiana* and *Yunnanites* in China. The second NWP clade consisting of *Sphenarium* and *Prosphena* is recovered as sister to the African genera *Ochrophlegma* and *Tanita*, both of which belong to the subtribe Pyrgomorphina of the tribe Pyrgomorphini. Kevan (1978) mentioned that some members of Pyrgomorphini, particularly the African genus *Chirindites* in the subtribe Parasphenina, convergently evolved similarities in size, form, and variation in color and even exhibit sexual

dimorphism where the males are often as large or even larger than females. He also mentioned that the type species of the African genus *Parasphena* in the subtribe Parasphenina was first described within *Sphenarium*. Finally, he stated some larger specimens of the African genus *Pyrgomorphella* (Pyrgomorphini: Pyrgomorphina) were reminiscent with the less robust Sphenariini. These claims were proposed without any phylogenetic method and were based on his vast experience of working with Pyrgomorphidae worldwide. In many cases Kevan's claims are reflected in the phylogeny (Chapter 6) but in others they do not have any phylogenetic signal.

The third NWP clade I recovered consists of the tribes Ichthiacridini (*Ichthiacris* and *Sphenacris*) (red in figs. 5.3 and 5.4) and Ichthyotettigini (*Pyrgotettix*, *Sphenotettix*, *Piscacris* and *Ichthyotettix*) (orange in figs. 5.3 and 5.4), each of which is found to be monophyletic. Both share cylindrical bodies, presence of columellae (small, paired, sclerotic structure on the floor of the genital chamber, situated near the base of the egg-guide. It vertically connects the postvaginal sclerite with the upper surface of the subgenital plate), and the extreme reduction of tegmina. They can be distinguished from each other by the rugose integument with small tubercles and a longer fastigium in Ichthiacridini and the smooth integument and short fastigium in Ichthyotettigini (Kevan et al. 1971). Sanabria-Urbán et al. (2015, 2017) used *Sphenacris*, *Pyrgotettix* and *Sphenotettix* as outgroups for an analysis focusing on the species-level relationships within *Sphenarium* and recovered them as a monophyletic group. As Kevan et al. (1964) and Kevan (1978) stated, Ichthiacridini is found in Northwestern and Central Mexico, in lower and more arid regions whereas Ichthyotettigini is found in Central to Southern Mexico at higher elevations and/or less arid conditions. These two tribes overlap very little in Central Mexico.

5.4.2 Dated phylogeny and biogeography

I estimate that the ancestral Pyrgomorphoidea diverged from the ancestral Acridoidea between 141 ± 18 mya, from the Late Jurassic to the Early Cretaceous, and it began to diversify in the Early Cretaceous (between 139 and 104 mya) according to the results of the BEAST analysis (fig. 5.5). During the Late Jurassic, Africa, Madagascar, India, Australia, Antarctica and South America were still connected as a supercontinent Gondwana. The earliest diverging lineage within Pyrgomorphidae is the genus *Psedna*, which includes stick-like grasshoppers endemic to Australia. The next lineage that diverged near the base of the phylogeny is a monophyletic group consisting of *Dictyophorus* (Africa), *Monistria* (Australia) and *Desmoptera* (India, Tropical Asia and Australia). Because of the distribution patterns of these genera, the most likely model selected using BioGeoBEARS (DIVALIKE+J) inferred that the ancestral range of the entire family was Australia (fig. 5.6). However, because our taxon sampling is not very broad, this inference should not be accepted at its face value. A more reasonable inference would be that the ancestral range of the early pyrgomorphs was somewhere in Gondwana. Later, during the Cretaceous, there was a major range expansion northwards towards Temperate Asia, according to the BioGeoBEARS analysis (fig. 5.6), but at this time, there was no direct route of colonization. Again, because our taxon sampling is lacking several African representatives, a more reasonable explanation would be northerly expansion and diversification in Africa, followed by the range expansion to Arabian Peninsula and then Temperate Asia.

There were two colonization events that gave rise to the New World Pyrgomorphidae. The first colonization of the New World was by the common ancestor of *Jaragua* and *Algete*, or the

ancestral Omurini, which took place in the Cretaceous (fig. 5.7). Our dated phylogeny estimated the divergence of this clade to be between 112 and 81 mya (green in fig. 5.5). Depending on the divergence time, it is possible to invoke either vicariance or dispersal. Specifically, at this period, South American continent and African continent were either together (early date) or recently split (later date). Thus, it is difficult to determine which process was responsible for the patterns we observe today (fig. 5.7). There are other organisms with similar patterns and explanations based in vicariance or dispersal scenarios between Africa and South America. Qin et al. (1998) found that wax scale insects (Hemiptera: Coccidae) have the majority of species in either Africa or South America. They hypothesized an origin in the combined African-South American area at least 97 mya and considered vicariance as the preferred explanation. For frogs, Feller & Hedges (1998) suggested that families Hyloidea (South America) and Ranoidea (Africa) diverged when South America separated from Africa in the mid Cretaceous (~105 mya). In the case of the turtle family Pelomedusoidae, Noonan (2000) tested the hypothesis that their speciation was due to vicariance by the separation of South America and Africa. He found evidence to suggest that the present-day distribution of these turtles together with their phylogenetic relationships could be explained with extinctions and the extant taxa are relicts of an originally widespread group.

After this initial colonization, this lineage probably diversified giving rise to several groups, one of which colonized the Caribbean (Hispaniola Island) about 69 mya (Campanian/Maastrichtian in Late Cretaceous) to give rise to the present day *Jaragua* (fig. 5.7). Regarding the dispersal from northern South America to the Caribbean, Rosen (1976) postulated that in the Late Mesozoic – the Early Cenozoic (70-60 mya), the proto-Antilles (situated where Costa Rica and Panama are currently located) moved to the east and originated the Antillean archipelago. MacPhee & Iturralde-Vinent (2005) argued that terrestrial vertebrates were able to disperse to

islands in the Caribbean at any time, and the actual islands of Greater Antilles (Hispaniola Island among them) are younger than ~40 mya (Middle Eocene). Earlier islands must have existed but probably are now submerged. Morrone (2017) argued that during the Cretaceous, there were three uplift events with potential of create land bridges between North America / South America with the Cretaceous Antillean island arc. The most likely is the Late Campanian/Early Maastrichtian uplift event (75-66 mya). Graham (2003) considered the existence of a Cretaceous volcanic island arc with an extension from Ecuador in the south to Mexico/Chortís block in the north that was gradually moving through the area between North and South America towards the Bahamas platform in the Middle Eocene. During this 70 my period (110 -70 mya), there is evidence of complex patterns of separation and collision and emergence and submergence. He concluded that although both vicariance and dispersal could happen, the latter was the key driver for diversification. Meanwhile, there were continued diversifications of pyrgomorph lineages in Africa, giving rise to *Caprorhinus*, *Colemania*, *Phymateus* and *Poekilocerus*.

According to the BioGeoBEARS analysis, there was a second dispersal event from Africa to the New World about 69 mya (fig. 5.8). The analysis suggests that the common ancestor of Ichthiacridini, Ichthyotettigini, and a clade consisting of *Sphenarium*, *Prosphena*, *Ochrophlegma*, and *Tanita*, colonized North and Central America from Africa. However, this pattern requires more assumptions than the first dispersal event that gave rise to Omurini because of two main issues. By the end of the Cretaceous when this dispersal event took place, there was no direct connection between Africa and North America, which means that the dispersal must have taken place through the westward transatlantic colonization from Africa to South America. This lineage must have colonized northward to give rise to the present-day genera in North and Central America. Thus, the inference made by this biogeographical analysis makes an implicit

assumption of connection by South America. This, however, raises another problem because there is currently no pyrgomorph species in South America that has taxonomic affinities to Ichthiacridini, Ichthyotettigini, *Spenarium* and *Parasphena*. This means that we need to invoke extinction for this ancestral lineage that crossed the Atlantic Ocean and gave rise to the North and Central American taxa (fig. 5.8). While the westward transatlantic colonization from Africa to South America could have been a rare event, Africa-South America faunal connection has been well documented. For example, there are different groups whose current distribution is explained by long-distance dispersal from Africa to South America, such as Caviomorph rodents through waif dispersal (~40 mya) (Antoine et al., 2011; Poux et al., 2006), monkeys (~36 mya) (Lynch-Alfaro, 2017; Bond et al., 2015), amphisbaenians and gekkotan lizards (Gamble et al., 2011) and the iconic Neotropical bird *Opisthocomus hoazin* (Mayr et al., 2011). The common ancestor that colonized the New World for the second time gave rise to two lineages. The first lineage comprised the Mexican tribes Ichthiacridini and Ichthyotettigini, which diversified *in situ*, the first one in Northern Mexico and the second one in Southern Mexico. The second lineage comprised a clade consisting of *Sphenarium* and *Prosphena*, and another clade consisting of *Ochrophlegma* and *Tanita.* Because both *Ochrophlegma* and *Tanita* are African, the observed pattern suggest that the common ancestor of these two African genera recolonized Africa from South America. There is another equally parsimonious explanation, which suggests that there were two separate westward colonization events from Africa, first by the common ancestor of Ichthiacridini and Ichthyotettigini, and another by the common ancestor of *Sphenarium* and *Prosphena*, but this scenario is less likely under the best-fit model selected by the BioGeoBEARS analysis.

For the genus *Sphenarium* (central Mexico to northwest Guatemala), Sanabria-Urbán et al. (2015, 2017) discussed that in most recent geological times there are drivers for diversification such as the Neogene formation of the Mexican Transvolcanic Belt (19-3 mya) which caused an increase in topographical complexity and later the Quaternary climatic shifts (2.6-0.01 mya) provoke shifts in distribution ranges in highlands and lowlands of Mexico. Certainly these events could have shaped distribution and diversification of the NWP genera other than *Sphenarium,* such as the ones belonging to tribes Ichthiacridini and Ichthyotettigini. We infer that the common ancestor of *Ochrophlegma* and *Tanita* recolonized the Old World from the New World, based on the results of the BioGeoBEARS analysis. While both *Sphenarium* and *Prosphena* are wingless, *Tanita* and *Ochrophlegma* include fully winged species. While the eastward transatlantic recolonization from South America to Africa seems far-fetched, it has been reported from many taxa. For example, SanMartín & Ronquist (2004) conducted an analysis to test the role of vicariance and dispersal in the composition of Southern Hemisphere biotas using 19 plant and 54 animal phylogenies. They found that dispersal could be more important than previously assumed. For the dispersal event from northern South America to Africa in the late Cretaceous-early Tertiary (70-60 mya), there are 4.09 dispersal events versus 1.54 events from Africa to northern South America.

The tectonic history and biota origin of South America and the Caribbean is old and complex. However, the amount of geological and phylogenetic evidence is overwhelming and I found our scenarios plausible and I consider that dispersal has played a significant role in the distribution and diversification of the NWP.

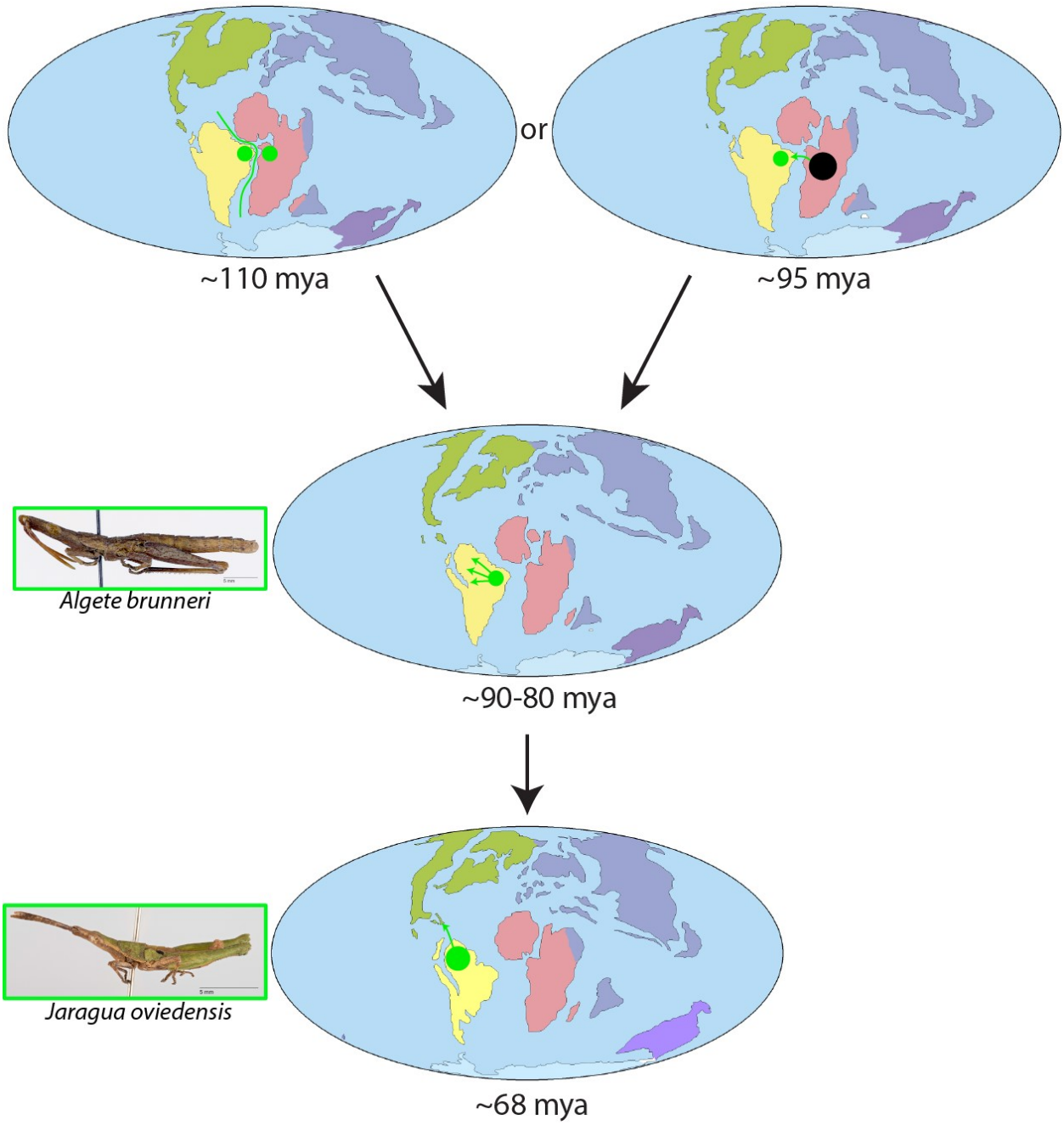

Figure 5.7. Scenarios explaining the origin of the NWP older clade (95 ± 15 mya) based in BioGeoBEARS DIVA-LIKE+J model. If the oldest age is considered (~110 mya), a vicariance event dividing South America and Africa is the most likely event to explain the cladogenesis. On the other hand, if both continents were already separated (~95 mya), a dispersal from Africa to South America is the most likely explanation. Once in South America (~90-80 mya), the clade diversified and expanded its range throughout the northern half of South America. Approximately 68 mya, a dispersal event from South America to the Caribbean gave rise to *Jaragua* lineage. Green shapes represent NWP lineages and black circle represents non-NWP ancestral pyrgomorphs.

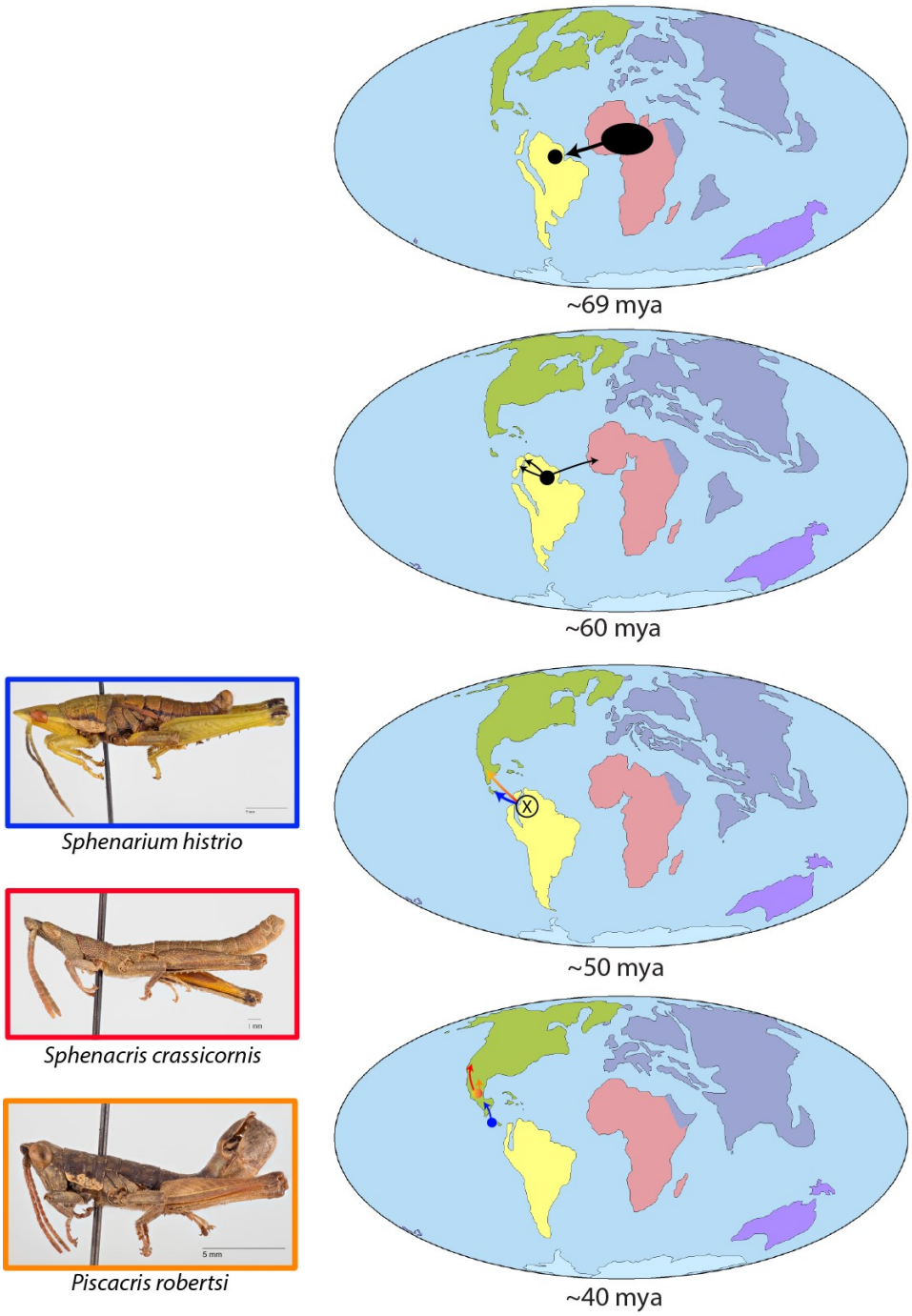

Figure 5.8. Scenario explaining the origin of the younger NWP clade (69 ± 15 mya) based in BioGeoBEARS DIVA-LIKE+J model. An ancestral lineage in Africa (black) dispersed to South America. Around 60 mya, one of the South America lineages dispersed back to Africa giving rise to *Ochrophlegma* and *Tanita*. Within South America, two northward dispersal events took place giving rise to two separate lineages (black). Around 50 mya, both northerly dispersal continued (blue and red/orange) and an extinction (black cross) of the South American lineage occurred. Around 40 mya, a *Sphenarium*/*Prosphena* lineage (blue) diversified in Central America and Southern Mexico whereas the Ichthyotetigini (orange) and Ichthiacridini (red) lineages continued diversifying to Central and Northern Mexico respectively.

5.5 Conclusions and future directions

Despite the low number of species of Pyrgomorphidae in the New World, its origin is very old and complex. I have provided evidence and rationale about the biogeography of the NWP based on a molecular phylogeny. I infer that the first wave of colonization was probably due to a vicariance event (split of Africa and South America) or a dispersal from West Africa to northern South America with a subsequent dispersal from South America to the Caribbean. It is probable that the first fauna of NWP was diverse at some point and we are now seeing the presence of only the relic lineages due to the antiquity of the group and probable extinction events. The second wave of colonization came by dispersal from West Africa to northern South America and then North America much later when the continents were already separated. The fauna found in North America (from Mexico to Costa Rica) consists of the most speciose NWP in genera such as *Sphenarium* (17 spp.) and *Ichthiacris* (8 spp.) Both genera harbor 60% of the current species diversity of the New World Pyrgomorphidae.

As a result of this analysis, I reject the theory by Kevan and Akbar (1964), which suggested that the NWP originated from Temperate Asia twice and subsequently dispersed to South America (fig. 5.2). Their claim of a relationship between the Chinese genera *Yunnanites* and *Mekongiana* with the Central American genera *Prosphena* and *Sphenarium* is not supported with molecular evidence. The morphological similarities among these genera are probably due to convergent evolution. Regarding the Orthacridini – Ichthiacridini/Ichthyotettigini relationship, I was not able to include genus *Orthacris* in the analysis and these two tribes were recovered in a clade with *Sphenarium* and *Prosphena* and two African Pyrgomorphini (*Ochrophlegma* and *Tanita*). Concerning the theory of Amédégnato (1993), which suggested that the NWP originated from Africa (fig. 5.2), we found general support although her original formulation was vague in terms

of specific Pyrgomorphidae taxa involved. Finally, although the theory by Mariño-Pérez and Song (2018) did not explicitly state the origin of the NWP, it could imply that the origin was from Asia and Madagascar based on their topology (fig. 5.2). In this sense, we reject their theory. However, they recovered the NWP in three separate clades as in this chapter although a different taxon sampling was used with only a small number of the NWP taxa. Thus, in terms of the paraphyly of the NWP, I concur with their conclusion.

In the future, an increased taxon sampling of the South American Omurini (*Omura* and *Minorissa*) will allow us to test the monophyly of Omurini. I need to include African and Malagassy Sphenariini (Sphenexiina and Rubelliina) to infer their placement in the phylogeny. Finally, I need to conduct a phylogeny based on morphology for the NWP with emphasis in the genus *Jaragua* and all the members of the South American tribe Omurini to update the current classification.

CHAPTER VI

PHYLOGENY-BASED NATURAL CLASSIFICATION OF THE FAMILY PYRGOMORPHIDAE

6.1 Introduction

The family Pyrgomorphidae is currently divided in two subfamilies (Pyrgomorphinae and Orthacridinae) (Cigliano et al. 2018). As outlined in Chapter 2, this division basically reflects the classification proposed by Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975), who arranged the family into two groups called, A and B, based on his intepretation of the diversity. Additionally, groups A and B were further divided in 4 and 6 series, respectively, with a total of 30 tribes (tribe Petasidini was split from Monistriini later by Key, 1985) collectively included in the family (Table 6.1). Kevan was an excellent taxonomist who spent many decades studying the diversity of Pyrgomorphidae, but he was an evolutionary taxonomist. Unlike modern systematists who study the diversity in a phylogenetic framework, evolutionary taxonomists would tend to rely heavily on their own expertise and did not adopt the newly emerging field of phylogenetic systematics that became a mainstream concept after the publication of Willi Hennig's (1966) influential treastise, *Phylogenetic Systematics*. As such, Kevan's taxonomic concepts on Pyrgomorphidae drew heavily from his own expertise and experience, rather than character-based phylogenetic methods. Thus, many of Kevan's tribes were created from his own authoritarian views, and unfortunately included many exceptions. However, Kevan was very careful and meticulous and his understanding of the internal male genitalia of Pyrgomorphidae was very sophisticated and often led to proper groupings that would be later shown to be monophyletic.

While Chapter 4 produced the first cladistic analysis of Pyrgomorphidae based on morphology, it suffered from the lack of taxon sampling. As I have shown in Chapter 5, some

of the morphological characters that I used previously were influenced by convergent evolution. Because the results from Chapters 4 and 5 represent a partial glimpse in to the phylogenetic diversity of Pyrgomorphidae, there is a need to expand taxon sampling to the fullest possible. Also, it is important to assess the phylogenetic utility of the characters that Kevan emphasized in his scheme. This way, it is possible to objectively test the monophyly of Kevan's groups A and B, as well as the 10 series that he proposed.

In this chapter, I present the most comprehensive phylogeny of Pyrgomorphidae based on morphology. I have reevaluated all the characters and states that I have previously published (Mariño-Pérez and Song 2018), and reexamined all of the characters that Kevan used for making his classification. Character coding has been influenced by the insights drawn from the results presented in Chapters 4 and 5. This new and comprehensive phylogeny critically tests Kevan's concepts and groups, series, and tribes in a phylogenetic framework.

Table 6.1. Summary of Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975) classification.

Group	Series	Tribe
A	I	Fijipyrgini
		Verduliini
		Brunniellini
		Psednurini
		Mitricephalini
	II	Geloiini
		Sagittacridini
		Gymnohippini
		Malagasphenini
	III	Chapmanacridini
		Ichthiacridini
		Ichthyotettigini
		Orthacridini
		Popoviini
	IV	Nereniini
B	V	Desmopterini
		Monistriini
	VI	Chlorizeini
		Poekilocerini
		Phymateini
	VII	Schulthessiini
		Taphronotini
		Dictyophorini
	VIII	Tagastini
		Pseudomorphacridini
		Atractomorphini
	IX	Sphenariini
		Omurini
	X	Chrotogonini
		Pyrgomorphini

6.1.1 Classification of Pyrgomorphidae sensu Kevan

In order to understand the rationale behind Kevan's classification scheme as well as to provide context to compare with the results of the comprehensive phylogenetic analysis, I summarize below the descriptions, characters, and distribution of the groups, sections, and tribes established by Kevan (Table 6.1). When appropriate, I also highlight the relationships that Kevan discussed in his works (Kevan et al. 1969,1970, 1971, 1972, 1974, 1975).

Group A. The species in this group are characterized by large metasternal pits both open and close, usually cylindrical or elongate body form, and hind femur often with both dorsal and ventral basal lobes subequally produced or with the dorsal lobe more prominent. These species are primarily distributed in "Gondawanian" areas, and absent from Palearctic region and South America but there are some representatives in Mexico. They are very poorly represented in the African continent. The Group A is divided into four series.

> **Series I.** A miscellaneous assemblage of anomalous tribes with the Indo-Malayan, Australian and Pacific Islands distribution. In general, this series includes fully winged species of the Group A. All pyrgomorph species with the galeae of the maxillae turn forward over the labrum are included here. The Series I includes 5 tribes (fig. 6.1).
>
> **Tribe 1. Fijipyrgini** *General morphology*: Body cylindrical, slender and with the fastigium of vertex long and acute. Galeae of maxillae turned forward to slightly overlap the margin of the labrum. Tegmina and wings well developed. Male terminalia specialized. *Distribution*: Fiji Islands. *Comments*: Certain features of external morphology and internal genitalia suggest possible relationships with the tribes Verduliini and Mitricephalini. The large central membrane of ectophallus probably suggests an affinity to the tribe Nereniini.

Tribe 2. Verduliini. *General morphology*: Body cylindrical with the fastigium of vertex of moderate length to very short and obtuse. Tegmina and wings fully developed to micropterous. Male terminalia not specialized. Epiphallus with prominent anterior projections. Basal emergination of cingulum extremely large and deep. Aedeagal valves large, denticulate. Reduced spermathecal. Postvaginal sclerite with a peculiarly sclerotized ornamentation. *Distribution*: New Guinea Island, Moluccas Islands and Philippines.

Tribe 3. Brunniellini. *General morphology*: Body elongate, slender with the fastigium of vertex acute. Galeae of maxillae turned forwards to overlap the margin of the labrum. Tegmina and wings fully developed. Lophi uniquely rod-like form. Subgenital plate long and narrow. *Distribution*: Philippines. *Comments*: Certain features of this anomalous tribe suggest affinities to the tribe Verduliini such as pointed apodemal plates and the ventral processes of the endophallic apodemes. The slender form and the condition of galeae suggest a relationship with the tribe Psednurini.

Tribe 4. Psednurini. *General morphology*: Body very long and slender, bacilliform. Fastigium of vertex greatly elongate. Galeae of maxillae modified and turned forward over the labrum. Tegmina and wings very rarely fully developed, sometimes scaly and usually absent. Subgenital plate very elongate. Columellae present. *Distribution*: Australia. *Comments*: This tribe has similarities with Brunniellini (galeae and subgenital plate) and some affinities with tribe Verduliini.

Tribe 5. Mitricephalini. *General morphology*: Body elongate-cylindrical with the fastigium of vertex very short. Tegmina and wings well developed but never reaching the tip of abdomen. Male genitalia specialized. Reduced spermatheca,

columellae absent. *Distribution*: Indonesia, Malaysia. *Comments*: This tribe may have a relationship with the tribe Geloiini due to similarities in aedeagal sclerites. The reduced spermatheca suggests an affinity to the tribe Verduliini.

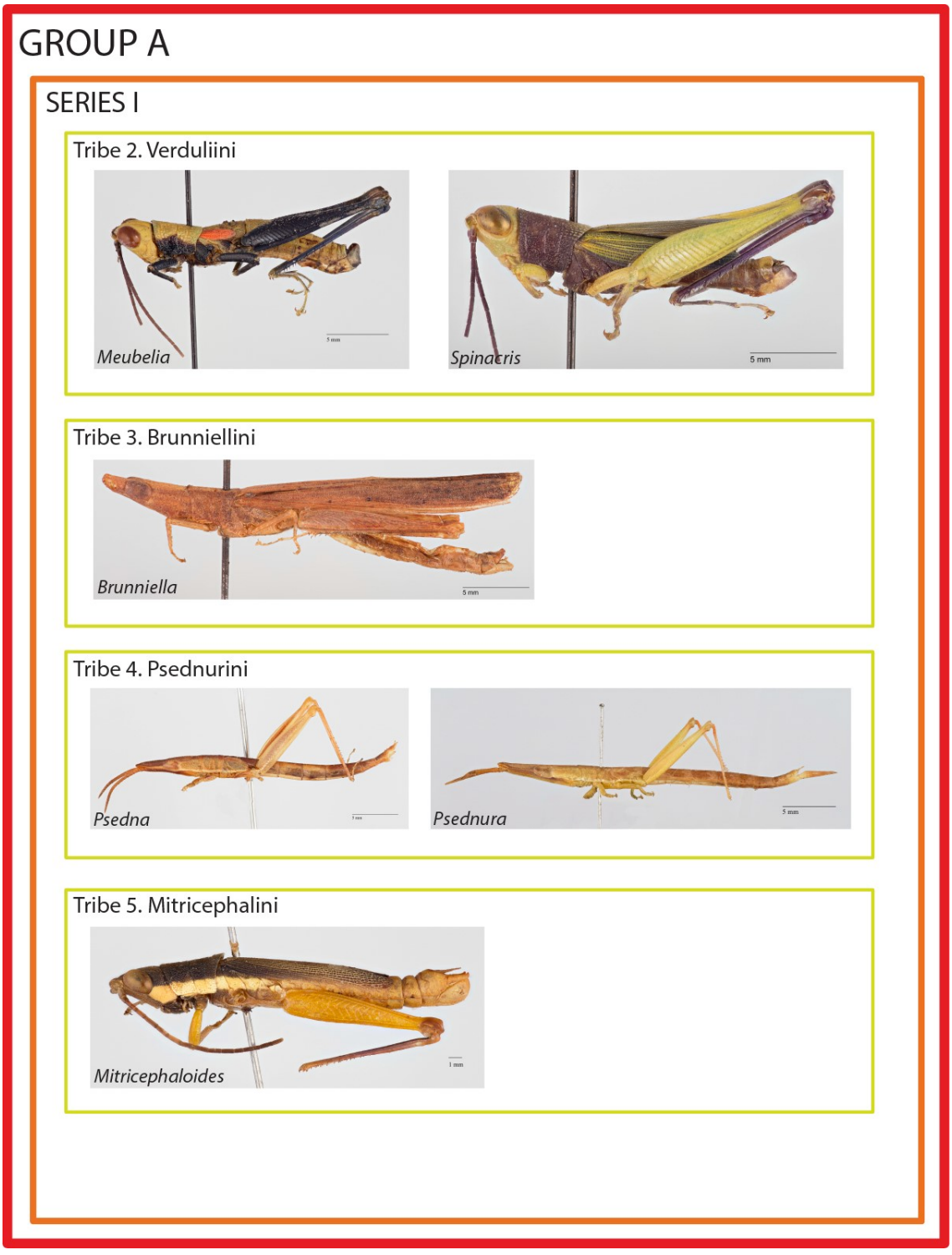

Figure 6.1. Group A. Series I. Tribes Verduliini, Brunnellini, Psednurini and Mitricephalini.

Series II. All species in this series are from Madagascar and are apterous or micropterous. They share an excised frontal costa below the fastigium of vertex in a lateral view (except *Gymnohippus*). Series II consists of four tribes (fig. 6.2).

Tribe 6. Geloiini. *General morphology*: Body elongate, cylindrical. Integument frequently striated. Fastigium of vertex moderately short and triangular to long and acute. Tegmina and wings absent or minute (scale-like). Male terminalia specialized. Epiphallus unspecialized. Columellae absent. *Distribution*: Madagascar. *Comments*: There are similarities in external genitalia and phallic structures with the tribe Mitricephalini.

Tribe 7. Sagittacridini. *General morphology*: Body elongate and cylindrical to elongate and fusiform. Integument smooth. Fastigium of vertex long and acute. Tegmina and hind wings absent or scale-like, Male terminalia unspecialized. Columellae absent. Spermatheca large. *Distribution*: Madagascar. *Comments*: This tribe could be related to the tribe Geloiini due to similarities in external morphology. Also, there are similiarities in cingulum with the tribe Gymnohippini.

Tribe 8. Gymnohippini. *General morphology*: Body fusiform or short and robustly cylindrical. Integument granular. Fastigium of vertex acute and triangular to short and blunt. Tegmina and wings absent or highly reduced. Male terminalia unspecialized. Epiphallus unspecialized. Basal emargination very shallow. Apodemal plates rounded. Ventral processes of cingulum lacking. Columellae absent. *Distribution*: Madagascar. *Comments*: This tribe appears to be related to the tribes Sagittacridini and Malagasphenini.

Tribe 9. Malagasphenini. *General morphology*: Body cylindrical but not elongate. Integument punctured. Fastigium of vertex short and acute. Tegmina and

wings highly reduced (minute scales). Male terminalia unspecialized. *Distribution*: Madagascar. *Comments*: This tribe is similar to the tribe Gymnohippini in external morphology. Other relationships appear to be with the tribes Orthacridini and Popoviini.

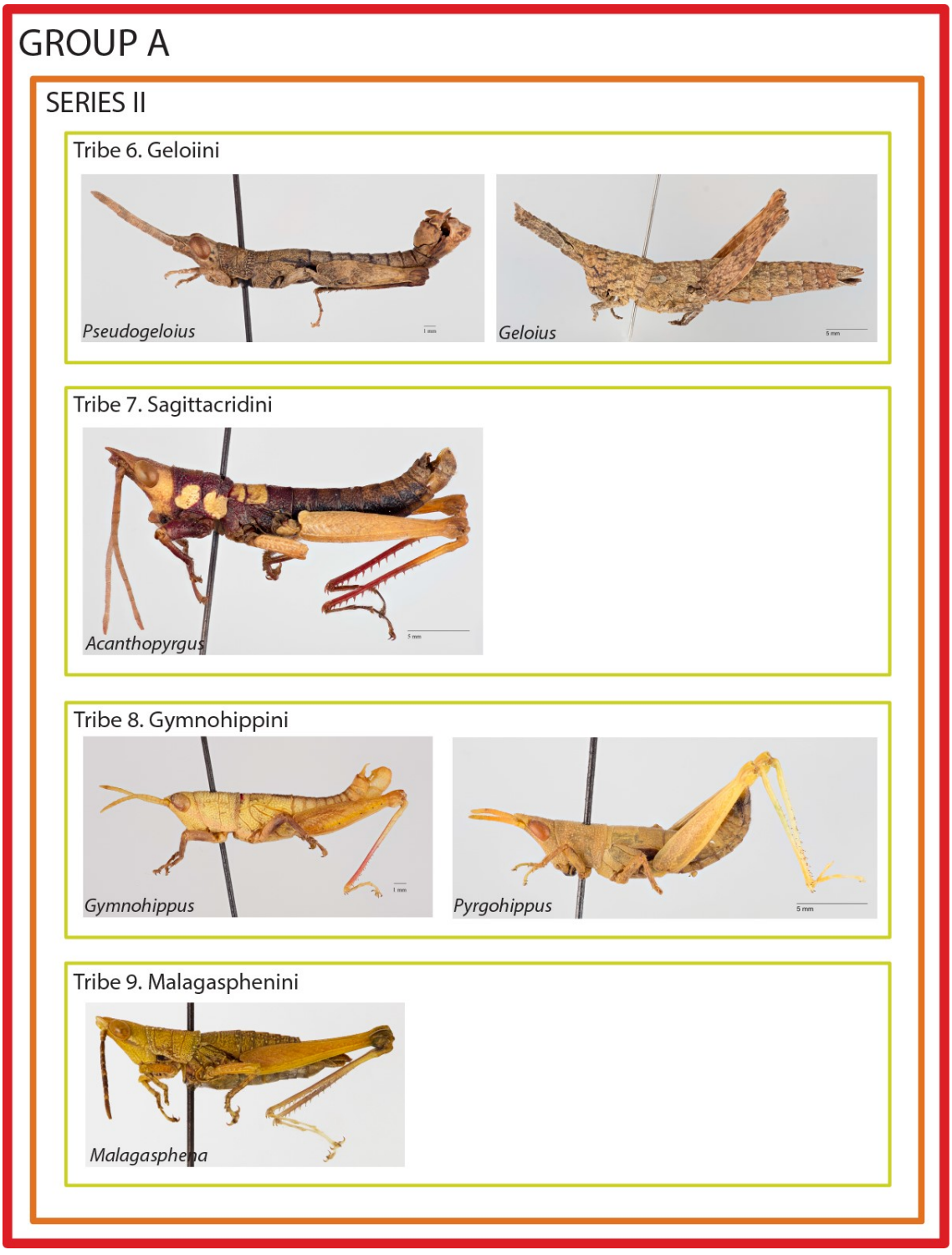

Figure 6.2. Group A. Series II. Tribes Geloiini, Sagittacridini, Gymnohippini and Malagasphenini.

Series III. Members of this series occur in Mexico, continental Africa (poorly represented), Madagascar, Southwestern and Southern Asia and Sri Lanka. The characters that unite tribes in this series are negative characters (the absence of a feature rather than the presence of a feature), and thus this series can be viewed as a "garbage group". It is composed of five tribes (fig. 6.3).

Tribe 10. Chapmanacridini. *General morphology*: Body elongate-cylindrical with smooth integument. Fastigium of vertex triangular and short. Tegmina present as vestigial pads. Columellae absent. *Distribution*: West Africa. *Comments*: This tribe has affinities with the tribe Geloiini due to similarities in internal male genitalia.

Tribe 11. Ichthiacridini. *General morphology*: Body cylindrical and elongate to fusiform with small tubercles. Fastigum of vertex triangular usually long and acute. Tegmina present as vestigial pads or absent. Male abdominal terminalia unspecialized. Internal male genitalia unspecialized. Columellae present. *Distribution*: Mexico. *Comments*: This tribe has affinities in external morphology with the tribes Ichtyotettigini and Orthacridini.

Tribe 12. Ichthyotettigini. *General morphology*: Body cylindrical or slightly fusiform. Integument smooth. Fastigium of vertex short and triangular. Tegmina absent. Male terminalia often protruded. Epiphallus sometimes highly specialized. Columellae present. *Distribution*: Mexico. *Comments*: This tribe has affinities with the tribe Ichthiacridini.

Tribe 13. Orthacridini. *General morphology*: Body cylindrical to slightly fusiform. Integument punctate or granular. Fastigium of vertex short and triangular to elongate acute. Tegmina and wings absent or reduced to scales. Male genitalia unspecialized. Columellae absent. *Distribution*: Southeast and Southern Asia,

Northeastern Africa, Comoro Islands and Madagascar. *Comments*: Its affinities appear to be to other tribes of Series III. These are also possibly connected to the tribes Mitricephalini and Chlorizeini.

Tribe 14. Popoviini. *General morphology*: Body cylindrical to slightly fusiform. Fastigium of vertex short to long. Micropterous and apterous. Epiphallus of convential form. Columellae absent. *Distribution*: South India, Southwest Arabia and Somalia. *Comments*: This tribe shows resemblances with tribe Orthacridini.

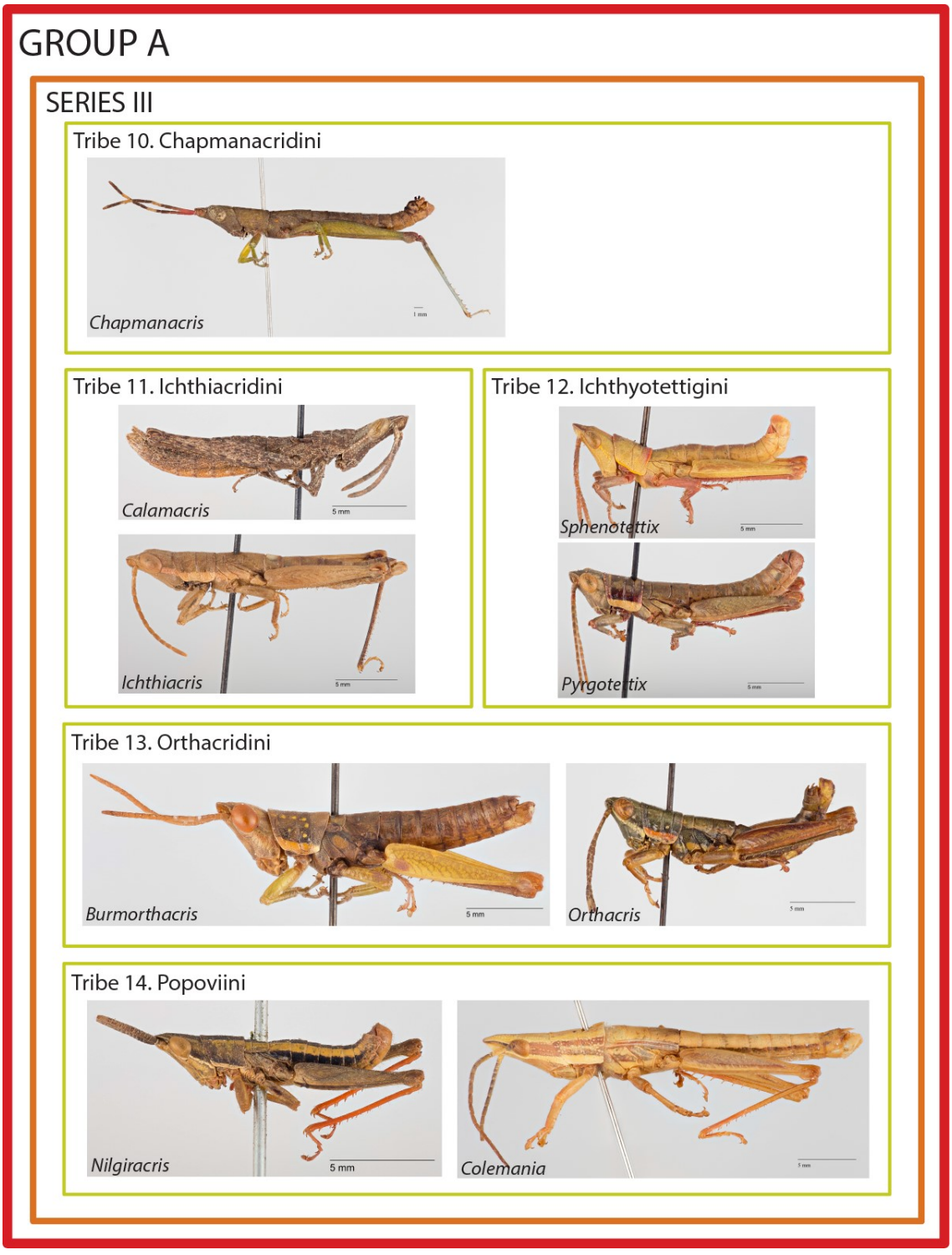

Figure 6.3. Group A. Series III. Tribes Chapmanacridini, Ichthiacridini, Ichthyotettigini, Orthacrdini and Popoviini.

Series IV. This series includes species from New Guinea Islands and other areas of Southwestern Pacific. All of the species in this series are apterous except *Megra*, and all apterous genera except *Nerenia* possess the fastigium of vertex short or transverse. Series IV is comprised of a single tribe (fig 6.4).

Tribe 15. Nereniini. *General morphology*: Body cylindrical or almost. Integument granular or rugose. Fastigum of vertex very short and blunt. Epiphallus variable. Columellae absent. *Distribution*: New Guinea Islands and Southwestern Pacific Islands. *Comments*: This tribe has affinities with Verduliini and Orthacridini. Due to its distribution, it is possible that some relationships exist with the tribe Fijipyrgini.

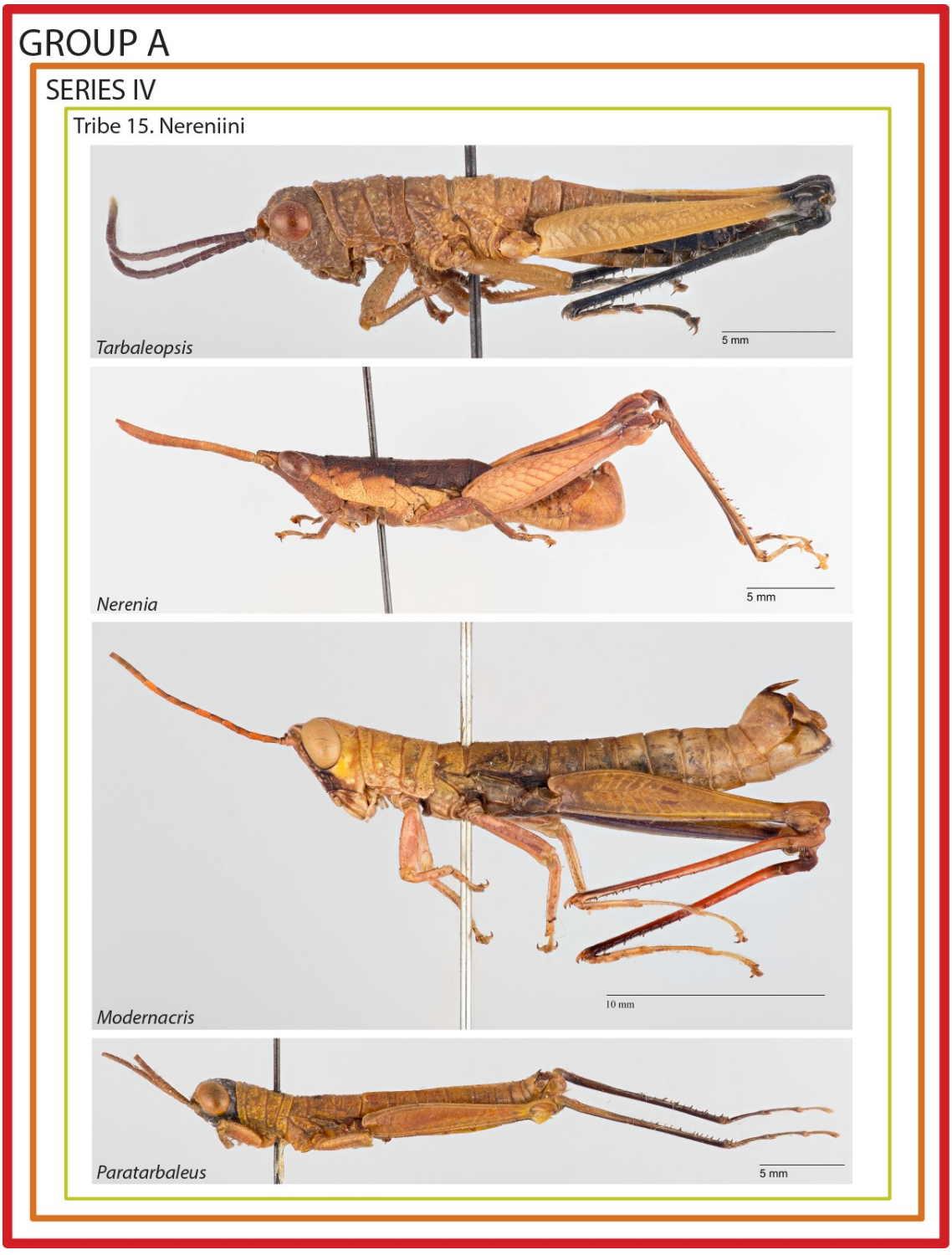

Figure 6.4. Group A. Series IV. Tribe Nereniini.

Group B. The species in this group are characterized by metasternal pits that are usually small and closed, body form that is usually fusiform or heavy and robust or both, pronotum sometimes armed with spines and tubercles, and hind femur always with ventral basal lobe more prominent than dorsal lobe. These species are predominantly distributed in circumtropical and subtropical regions with some species extending to temperate regions. They are very rich in African continent but with few species in Madagascar. The Australian Pyrgomorphidae except the tribe Psednurini belong to this Group. The Group B is divided in six series.

Series V. This series comprised two tribes of dissimilar external appearance but with similar distribution patterns. The endophallus in both tribes frequently has a strong development of dorsal inflections of the endophallic apodemes and specialized aedeagal valves. It is composed of two tribes (fig. 6.5).

Tribe 16. Desmopterini. *General morphology*: Body laterally compressed and slender. Integument finely rugose. Fastigium of vertex usually bluntly triangular. Tegmina rarely reduced, but never absent. Male genitalia unspecialized. *Distribution*: Northern Australia and South Pacific region to Philippines. *Comments*: This tribe has some affinities with the tribe Nereniini (elongate spermatheca) and has similarities in endophallus with the tribe Monistriini.

Tribe 17. Monistriini. *General morphology*: Body heavily built from fusiform to short and robust. Integument rugose or at least with some granular tubercles and pustules. Tegmina and wings usually reduced. Epiphallus uniform and unspecialized but with quadrate anterior projections. Columellae absent. *Distribution*: Australia. *Comments*: This tribe was later divided by Key (1985) into Monistriini and Petasidini. Originally the genera of this tribe were placed in the tribe Poekilocerini

and the affinities in external are evident but not in internal genitalia. There is an association to the tribe Desmopterini due to the similarities in endophallus. There are also some affinities in genitalia with the tribe Chlorizeini.

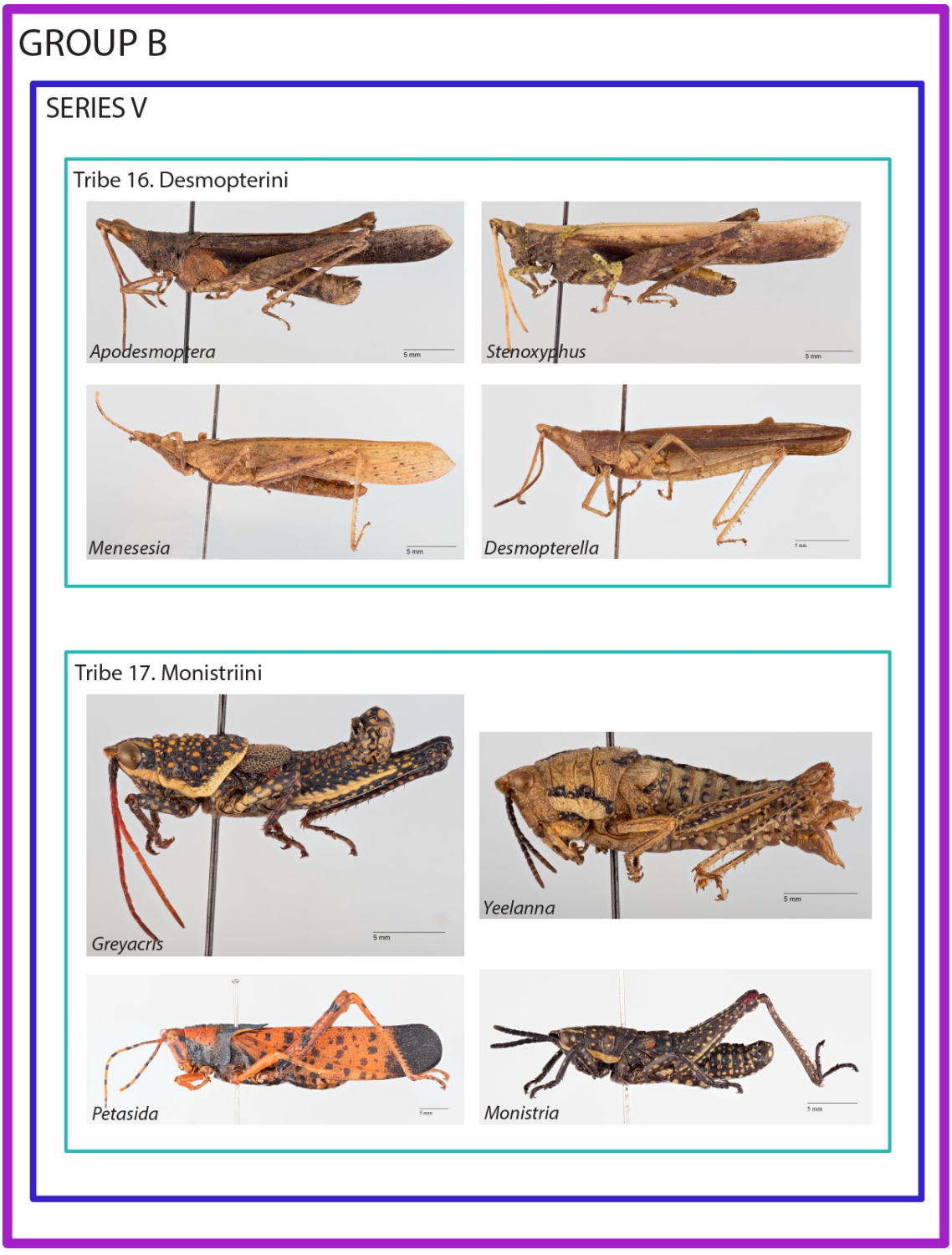

Figure 6.5. Group B. Series V. Tribes Desmopterini and Monistriini.

Series VI. This series is a heterogeneous assemblage, united more by the absence of characters than by the presence of particular features. The species in this series have tegmina and wings, which never absent, pronotum sometimes with spines and tubercles, epiphallus with conventional form and large lobe-like anterior pojections, and columella-like structures. These species are distributed in Africa, Madagascar, Socotra Island and continental southern Asia, but never on the island of Southeast Asia, Australia, or the New World. It consists of three tribes (fig. 6.6).

Tribe 18. Chlorizeini. *General morphology*: Body not heavily built with integument smooth or with small granular tubercles. Tegmina and wings usually not reaching the tip of abdomen. Wings not colored. Epiphallus with bridge constricted in the middle. Columella-like thickenings. *Distribution*: Southeast continental Asia, Madagascar and tropical Africa. *Comments*: Apart from the affinities with the tribes Poekilocerini and Phymateini, this tribe could be distantly related to the tribe Orthacridini. The female structures of *Burmorthacris* are reminiscent to the tribe Chorizeini. Also, it may be somewhat related to the tribe Tagastini.

Tribe 19. Poekilocerini. *General morphology*: Body large and robust, subfusiform. Integument smooth to granular and slightly postulate. Pronotum never with spines or tubercles. Tegmina and wings well developed. Wings colored. Columellae-like thickenings. *Distribution*: India, some parts of Southwest Asia and Africa north of Equator. *Comments*: This tribe originally included many genera among which was the tribe Monistriini. Its internal genitalia are related to the tribes Chlorizeini and Phymateini.

Tribe 20. Phymateini. *General morphology*: Body moderate to usually large (largest Pyrgomorphidae). Integument smooth to rugose. Coloration often striking

with aposematic patterns on the abdomen. Fastigium of vertex short. Pronotum smooth or with spines and tubercles. Tegmina and wings always present. Wings colored. Columellae-like thickenings. *Distribution*: Sub-Saharan Africa, Madagascar and Socotra Island. *Comments*: The genus *Physemophorus* may be a link to Poekilocerini. However, this genus would seem to be close to *Zonocerus*.\

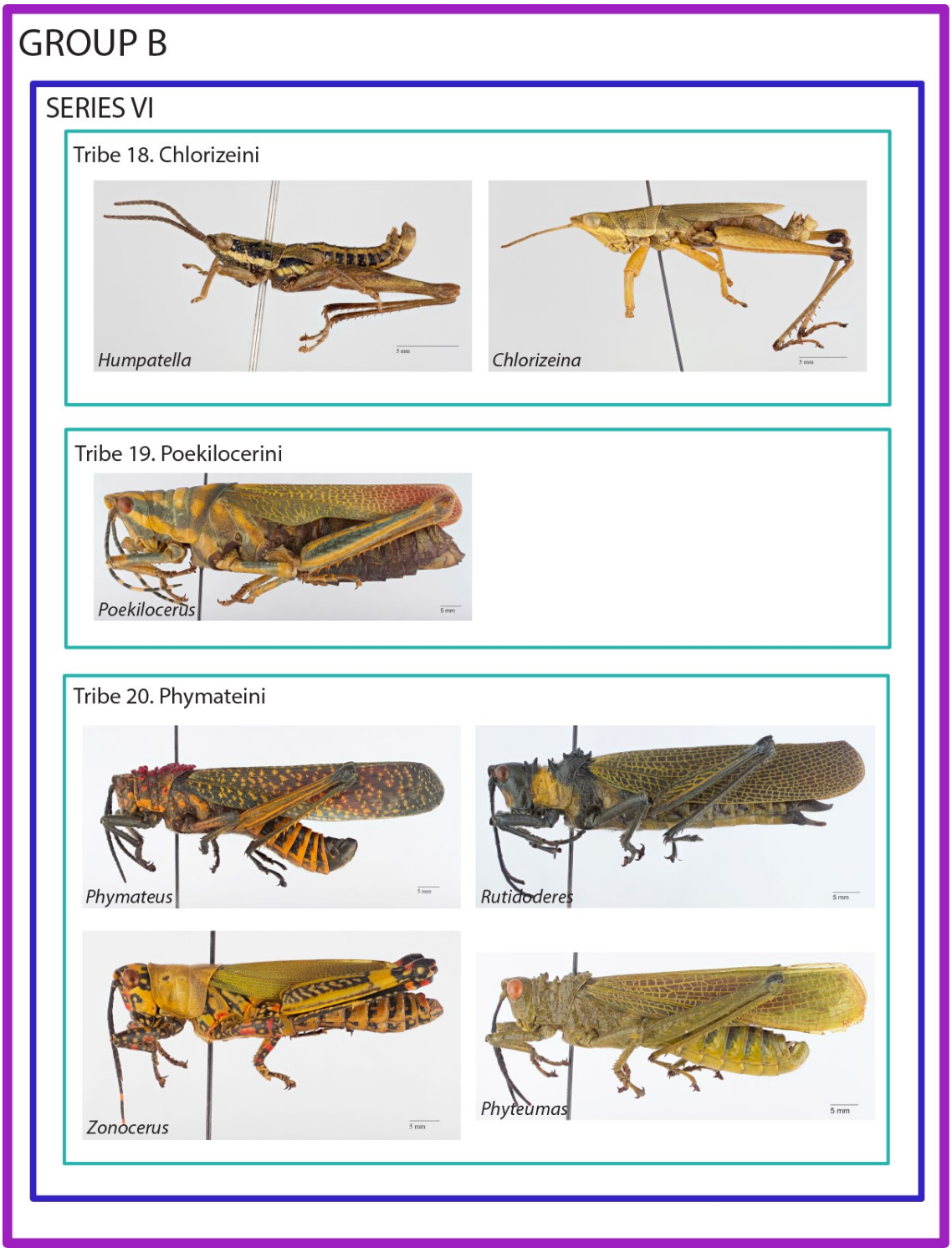

Figure 6.6. Group B. Series VI. Tribes Chlorizeini, Poekilocerini and Phymateini.

Series VII. Members of this series differ amongst each other in external morphology. With exception to the tribe Schulthessiini, all genera have a rugose or tuberculate pronotum. Most of the species in this series are moderate to large in size, often robust or heavily built. Their body forms range from fusiform usually fully winged. robust with a short blunt head, and sometimes with reduced tegmina. The Madagascar tribe Schulthessiini superficially resembles the tribe Atractomorphini. Members of this series share a spermatheca without a distinct apical pocket, but possess an extensive spermathecal appendage. These species are distributed in Sub-Saharan Africa, Madagascar and Southern Asia. This series consists of three tribes (fig. 6.7).

Tribe 21. Schulthessiini. *General morphology*: Body elongate-fusiform with integument finely rugose to smooth. Epiphallus unspecialized but with well-developed anterior projections. *Distribution*: Madagascar. *Comments*: This tribe externally resembles the tribe Atractomorphini, but the epiphallus and spematheca are quite different. The specialization of spermatheca probably relates it with the tribe Taphronotini.

Tribe 22. Taphronotini. *General morphology*: Body fusiform (*Taphronota*) or robust (*Aularches*). Integument rugose. Head strongly conical (*Taphronota*) or short and blunt (*Aularches*). Pronotum very rugose or tuberculate. Tegmina and wings fully developed and wings orange or red. Epiphallus unspecialized. *Distribution*: Sub-Saharan Africa and Southern Asia. *Comments*: Members of this tribe appear to be closely related to the tribe Dictyophorini.

Tribe 23. Dictyophorini. *General morphology*: Body robust with rugose integument and pronotum with tubercles. Head from conical to blunt. Tegmina and wings usually reduced. Wings red with black borders or entirely black. Epiphallus

rather unspecialized. Secondary diverticula of spermatheca highly developed. *Distribution*: Sub-Saharan Africa. *Comments*: It appears to be related to the tribe Taphronotini.

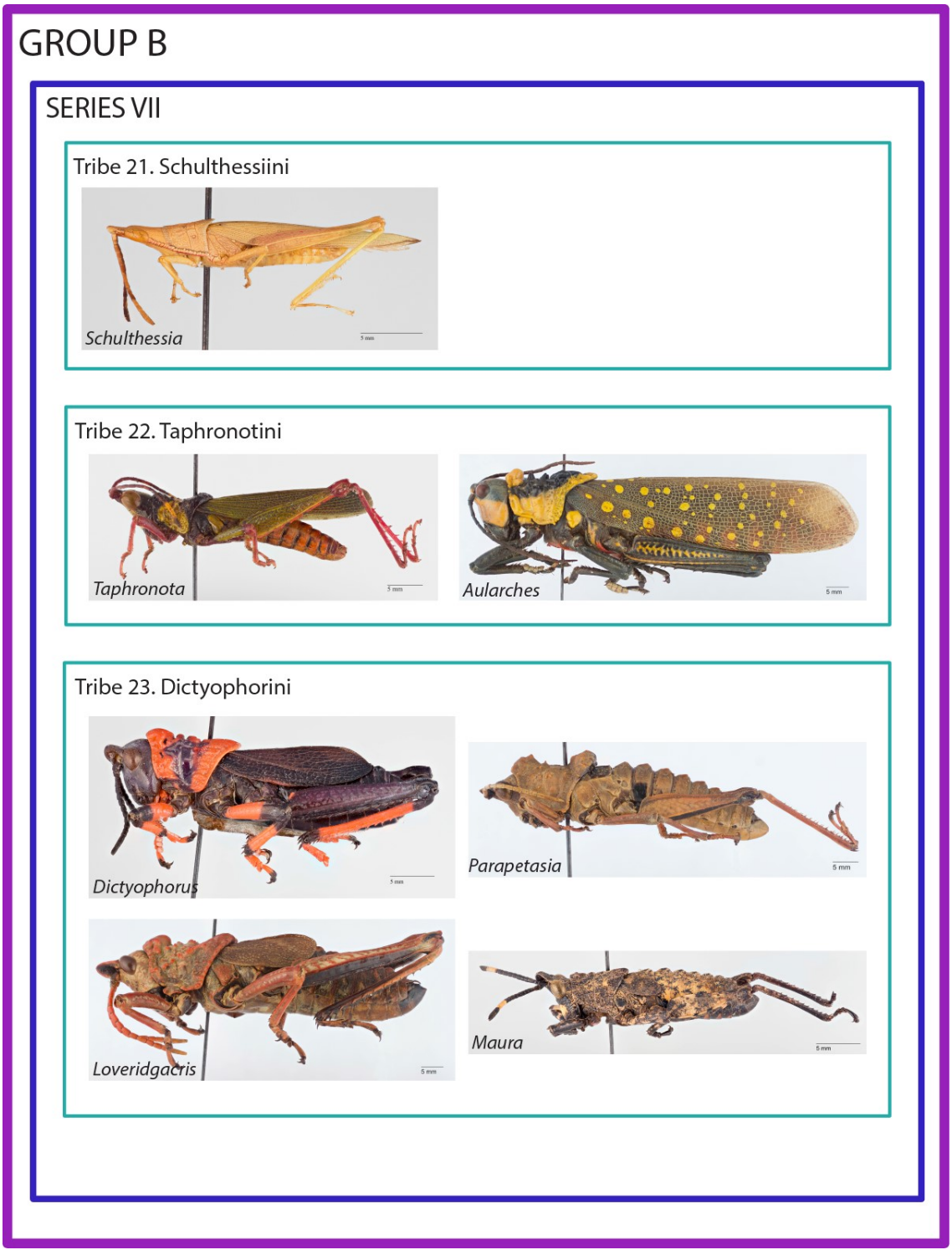

Figure 6.7. Group B. Series VII. Tribes Schulthessiini, Taphronotini and Dictyophorini.

Series VIII. This series includes three tribes from Southeast Asia (one with much wider distribution). All members are fusiform with a conical head and an oblique frons without any tubercles or spines. Tegmina and wings are well developed except in *Occidentosphena* which is apterous. Subgenital plate has columellae (fig. 6.8).

Tribe 24. Tagastini. *General morphology*: Body fusiform, integument smooth. Frons strongly oblique, slightly concave in profile. Fastigum of vertex not very acute. Tegmina tapering but no acutely pointed. Epiphallus unspecialized. *Distribution*: Southeast Asia. *Comments*: The closest relative appears to be the tribe Pseudomorphacridini from which they might be derived.

Tribe 25. Pseudomorphacridini. *General morphology*: Body robust, strongly fusiform. Integument finely rugose. Head strongly conical with a frons very oblique and an acute fastigium of vertex. Male cerci specialized. Epiphallus of specialized form with unique bifid lophi. *Distribution*: Continental Southeast Asia. *Comments*: This tribe appears to be related to the tribe Tagastini due to its similarities in cingulum. In external morphology, it resembles the tribe Atractomorphini and Schulthessiini (based on expanded and displaced external area of the hind femur).

Tribe 26. Atractomorphini. *General morphology*: Body fusiform to elongate-fusiform. Integument very finely rugose. Head strongly conical. Fastigium of vertex long. Epiphallus of particular form with fused bridge, lateral plates and lophi. Spermatheca "double" (wide spermathecal vesicle appendage leading into the vestibule, the spermathecal vesicle and caecum). Columellae present. *Distribution*: Africa (except Mediterranean areas), Madagacar, Asia, Pacific and Australia. *Comments*: The genus *Atractomorpha* has been grouped with the Madagascar tribe Schulthessiini and with the South American tribe Omurini.

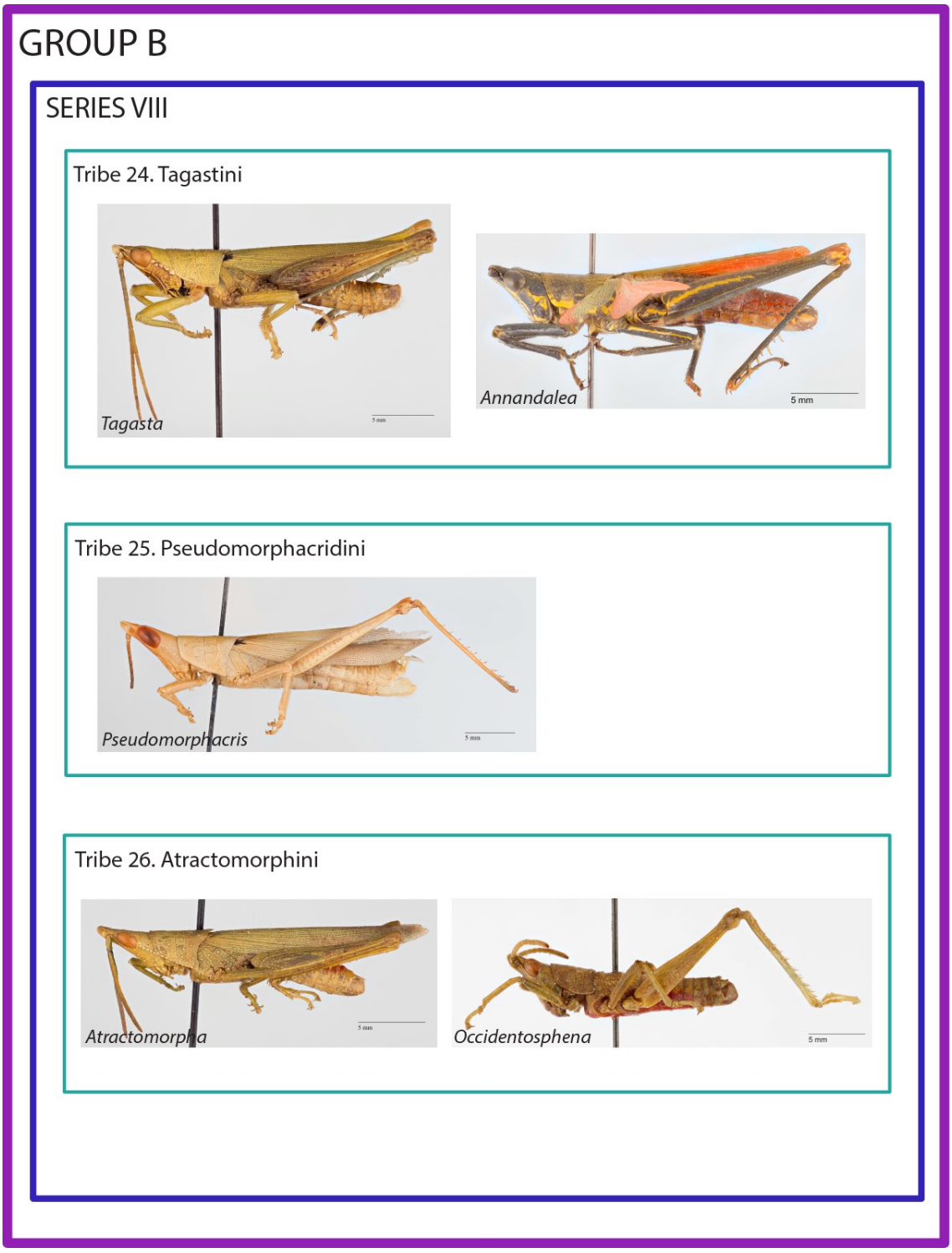

Figure 6.8. Group B. Series VIII. Tribes Tagastini, Pseudomorphacridini and Atractomorohini.

Series IX. This series comprises two tribes, one stout and strongly fusiform and the other more elongate. Members of this series are distributed in South America, Mexico to Costa Rica, Socotra Island, West Africa, Madagascar, and China (fig. 6.9).

Tribe 27. Sphenariini. *General morphology*: Body strongly fusiform to very short and robust. Integument smooth to granular. Head acute to obtuse. Fastigium of vertex long to short, blunt to pointed. Pronotum strongly widened posteriorly. Tegmina seldom fully developed. Epiphallus usually rectangular. Columellae present. *Distribution*: As in the series IX, but excluding South America. *Comments*: It appears to be somewhat relatd to the tribe Pyrgomorphini due to rectangular epiphallus.

Tribe 28. Omurini. *General morphology*: Body elongate-fusiform, sometimes depressed. Integument finely to rugose. Head elongate-conical. Frontal profile very oblique. Fastigium of vertex much longer than wide and usually acute. Pronotum widened posteriorly. Tegmina usually absent but if present then acuminate. Lateral plates of epiphallus long and narrow. Columellae absent. *Distribution*: Northern half of South America. *Comments*: This tribe may be related to the tribes Atractomorphini and Schulthessiini due to external morphology. It might be related to some Asian Sphenariini due similarities in epiphallus.

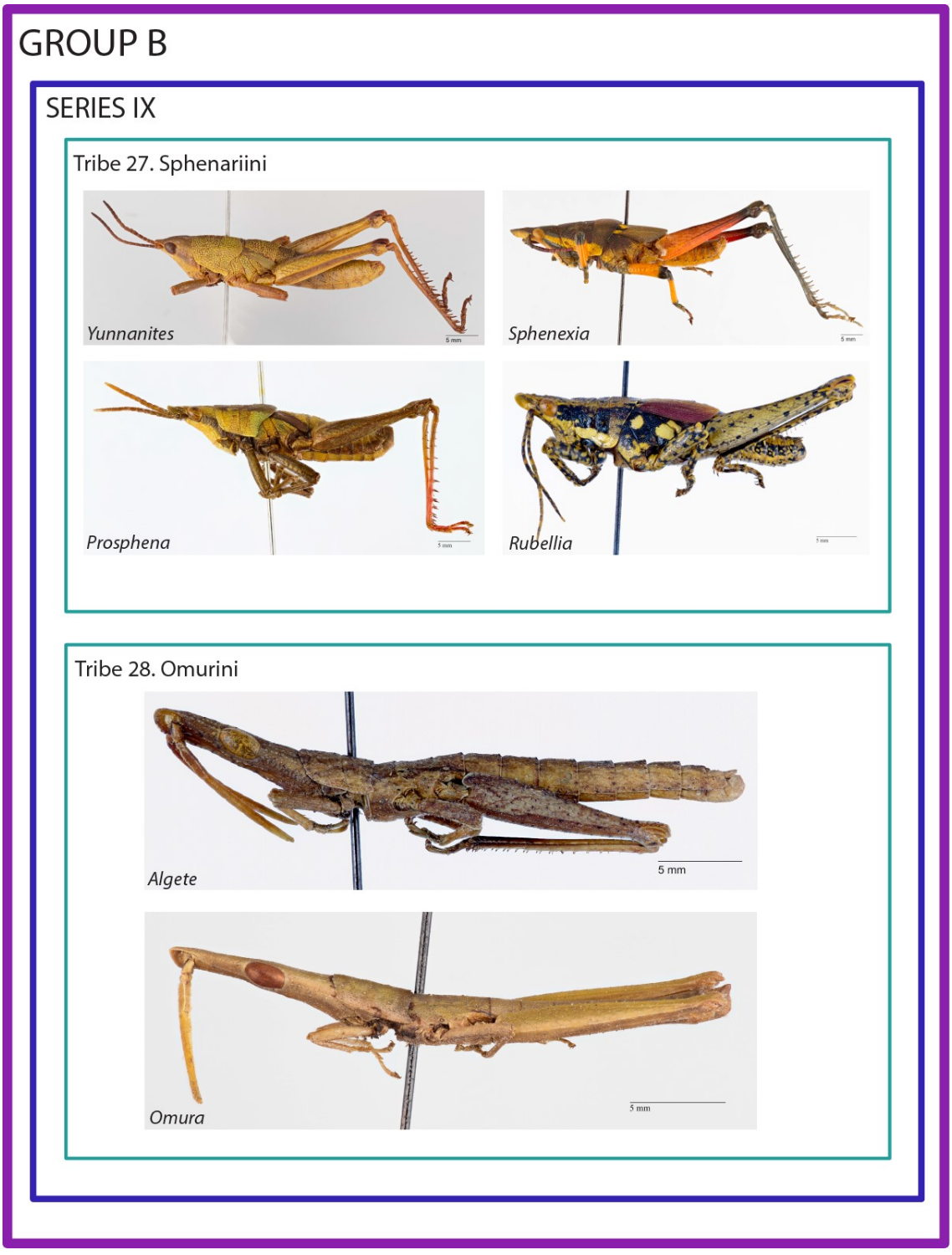

Figure 6.9. Group B. Series IX. Tribes Sphenariini and Omurini.

Series X. This series comprises two tribes but the first includes more genera than any other. They are mainly distributed in Africa but some are found in Mediterranean Region, Madagascar and continental Asia (fig. 6.10).

Tribe 29. Pyrgomorphini. *General morphology*: Body never large, usually small. Fusiform to elongate fusiform. Integument usually slightly rugose. Head conical, frontal profile oblique. Fastigium of vertex of moderate length not very acute. Pronotum not exceptionally widened posteriorly. Tegmina and wings variable. Male cerci simple. Epiphallus unspecialized with lateral plates of lophi expanded. Columellae absent or present. *Distribution*: Africa, Mediterranean, Madagascar, and Asia. *Comments*: This tribe could be related to the tribe Sphenariini due to its similarities in epiphallus.

Tribe 30. Chrotogonini. *General morphology*: Body never large and usually depressed. Integument strongly rugose. Head usually blunt but sometimes conical. Frontal profile not usually oblique. Pronotum very strongly divergent posteriorly. Prosternum collar-like. Epiphallus unspecialized. Columellae absent. *Distribution*: Africa, Southwest Asia to Pakistan. Indian subcontinent to Central Asia and China. *Comments*: This tribe probably has a common origin with the tribe Pyrgomorphini.

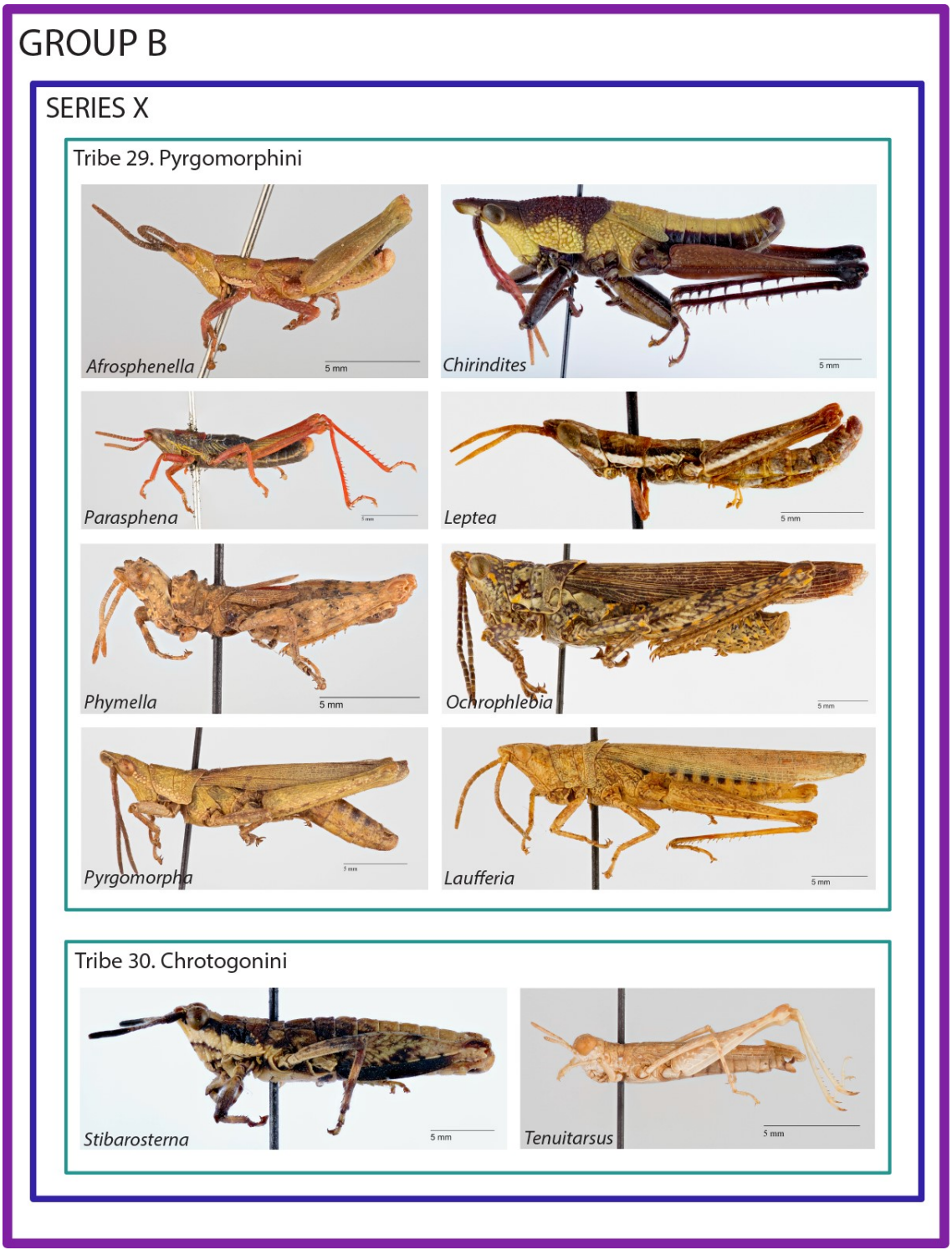

Figure 6.10. Group B. Series X. Tribes Pyrgomorphini and Chrotogonini.

6.2 Material and methods

6.2.1 Taxon sampling

In order to reconstruct a comprehensive phylogeny, I expanded previously published taxon sampling (Mariño-Pérez and Song 2018) by adding 5 new outgroup and 64 ingroup taxa. In total, the present taxon sampling included 113 terminals (8 outgroups and 105 ingroups). For outgroups I included 8 species representing 7 families (Tanaoceridae, Pneumoridae, Trigonopterygidae, Pyrgacrididae, Pamphagidae, Lentulidae and Acrididae). The ingroup sampling represented 29 out of 31 currently known tribes and 105 out of 148 genera (Table 6.2). I was not able to obtain specimen of the monotypic tribes Fijipyrgini (Fiji Islands) and Malagasphenini (Madagascar). To my knowledge these are only known from the type material. The specimens used in this study were borrowed from the following institutions: Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (ANSP); The Natural History Museum, London, UK (BMNH); the Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museum für Naturkunde, Berlin, Germany (MfN).

6.2.2 Character sampling

I used the great majority (117 out of 119) characters from Chapter 4 and added 20 new characters mainly from female genitalia. Other 12 characters dealing with general genitalia characteristics in Acridomorpha were taken from Song and Mariño-Pérez (2013). In total 149 characters were used in this chapter.

Table 6.2. Taxon sampling used in this study.

Family	Subfamily/Group	Series	Tribe	Species
Tanaoceridae				*Tanaocerus koebelei* Bruner, 1906
Pneumoridae				*Physemacris variolosa* (Linneaus, 1758)
Trigonopterygidae				*Trigonopteryx hopei* (Westwood, 1841)
Pyrgacrididae				*Pyrgacris descampsi* Kevan, 1976
Pamphagidae				*Prionotropis hystrix* (Germar, 1917)
Lentulidae				*Lentula* sp.
Acrididae				*Locusta migratoria* (Linneaus, 1758)
Acrididae				*Guaranacris specularis* (Bruner, 1906)
Pyrgomorphidae	Orthacridinae/A	I	Verduliini	*Meubelia leytensi*s Kevan, 1974 (Philippines)
				*Spinacris inermi*s Kevan, 1974 (Philippines)
			Brunniellini	*Brunniella antistes* Bolívar, 1905 (Philippines)
			Psednurini	*Psedna nana* (Rehn, 1953) (Australia)
				Psednura musgravei Rehn, 1953 (Australia)
				Propsednura eyrei Rehn, 1953 (Australia)
			Mitricephalini	*Mitricephaloides rhodopterus* (Miller, 1934) (Malaysia)
		II	Geloiini	*Pseudogeloius decorsei* (Bolívar, 1905) (Madagascar)
				Geloius nasutus Saussure, 1899 (Madagascar)
			Sagittacridini	*Acanthopyrgus finoti* (Bolívar, 1905) (Madagascar)
			Gymnohippini	*Gymnohippus marmoratus* Bruner, 1910 (Madagascar)
				Pyrgohippus pallidus Dirsh, 1963 (Madagascar)
		III	Chapmanacridini	*Chapmanacris sylvatica* Dirsh, 1959 (Ghana)
			Ichthiacridini	Calamacris clendoni Rehn, 1904 (Mexico)
				Ichthiacris aptera Hebard, 1932 (Mexico)
				Sphenacris crassicornis Bolívar, 1884 (Mexico)
			Ichthyotettigini	*Ichthyotettix mexicanus* (Saussure, 1859) (Mexico)
				*Piscacris roberts*i Kevan, Singh & Akbar, 1964 (Mexico)
				Pyrgotettix pueblensis Kevan, Singh & Akbar, 1964 (Mexico)
				Sphenotettix nobilis Kevan, Singh & Akbar, 1964 (Mexico)
			Orthacridini	*Acropyrgus cadeti* Descamps & Wintrebert, 1966 (Madagascar)
				Burmorthacris aptera Kevan, Singh & Akbar, 1964 (Myanmar)
				Neorthacris acuticeps acuticeps (Bolívar, 1902) (India)

Table 6.2. Continued

Family	Subfamily/Group	Series	Tribe	Species
				Orthacris incongruens Carl, 1916 (India)
				Ambositracris vittata (Kevan, Akbar & Singh, 1964) (Madagascar)
				Caprorhinus kevani Descamps & Wintrebert, 1966 (Madagascar)
				Dyscolorhinus squalinus Saussure, 1899 (Madagascar)
				Vittisphena somalica Kevan, 1956 (Somalia)
			Popoviini	*Colemania sphenarioides* Bolívar, 1910 (India)
				Nilgiracris raoi (Kevan, 1953) (India)
				Popovia salvadorae Uvarov, 1952 (Yemen)
		IV	Nereniini	*Tarbaleopsis hystrix* Kevan, 1966 (Papua New Guinea)
				Modernacris controversa Willemse, 1931 (Solomon Islands)
				Paratarbaleus novaeguineae (Ramme, 1930) (Papua New Guinea)
				Nerenia francoisi Bolívar, 1905 (New Caledonia)
	Pyrgomorphinae/B	V	Desmopterini	*Apodesmoptera mira* Rehn, 1951 (Philippines)
				Desmoptera novaeguineae (Haan, 1842) (Indonesia)
				Desmopterella angustata Ramme, 1941 (Papua New Guinea)
				Menesesia novaeguineae Willemse, 1922 (Papua New Guinea)
				Menesesiella occulta (Rehn, 1951) (Papua New Guinea)
				Stenoxyphus aurantiacus (Karsch, 1896) (Indonesia)
			Monistriini	*Greyacris picta (Sjöstedt, 1921) (Australia)*
				Monistria concinna (Walker, 1871) (Australia)
				Yeelanna argus (Rehn, 1953) (Australia)
			Petasidini	*Petasida ephippigera* White, 1845 (Australia)
		VI	Chlorizeini	*Chlorizeina unicolor* Brunner von Wattenwyl, 1893 (Myanmar)
				Pterorthacris subcallosa Uvarov, 1921 (india)
				Cawendia glabrata Karsch, 1888 (Tanzania)
				Humpatella huambae Uvarov, 1953 (Angola)
			Poekilocerini	*Poekilocerus pictus* (Fabricius, 1775) (India)
			Phymateini	Paraphymateus roffeyi Dirsh, 1962 (Somalia)
				Phymateus saxosus Coquerel, 1861 (Madagascar)
				Phyteumas purpurascens (Karsch, 1896) (Tanzania)
				Rutidoderes squarrosus (Linnaeus, 1771) (Ghana)
				Physemophorus sokotranus (Burr, 1898) (Socotra Island)
				*Zonocerus variegatu*s (Linnaeus, 1758) (Congo)

Table 6.2. Continued

Family	Subfamily/Group	Series	Tribe	Species
		VII	Schulthessiini	*Schulthessia biplagiata* Bolívar, 1905 (Madagascar)
			Taphronotini	*Aularches miliaris* (Linnaeus, 1758) (Thailand)
				Taphronota ferruginea (Fabricius, 1781) (Cameroon)
			Dictyophorini	*Camoensia insignis* Bolívar, 1882 (Angola)
				Dictyophorus spumans (Thunberg, 1787) (South Africa)
				Loveridgacris impotens (Karsch, 1888) (Tanzania)
				Maura rubroornata (Stål, 1855) (South Africa)
				Parapetasia femorata Bolívar, 1884 (Gabon)
		VIII	Tagastini	*Tagasta indica* Bolívar, 1905 (India)
				Annandalea haematoptera (Haan, 1842) (Indonesia)
			Pseudomorphacridini	*Pseudomorphacris notata* (Brunner von Wattenwyl, 1893) (Myanmar)
			Atractomorphini	*Atractomorpha aberrans* Karsch, 1888 (Congo)
				Occidentosphena ruandensis (Rehn, 1914) (Rwanda)
		IX	Sphenariini	*Mekongiella kingdoni* (Uvarov, 1937) (China)
				Yunnanites coriacea Uvarov, 1925 (China)
				Rubellia nigrosignata Stål, 1875 (Madagascar)
				Jaragua oviedensis Perez-Gelabert, Dominici & Hierro, 1995 (Dominican Republic)
				Sphenarium histrio Gerstaecker, 1884 (Mexico)
				Prosphena scudderi Bolívar, 1884 (Guatemala)
				Sphenexia fusiformis Karsch, 1896 (Tanzania)
				Xenephias socotranus Kevan, 1973 (Socotra Island)
			Omurini	*Algete brunneri* Bolívar, 1905 (Brazil)
				Minorissa pustulata Walker, 1870 (Venezuela)
				Omura congrua Walker, 1870 (Brazil)
		X	Chrotogonini	*Chrotogonus oxypterus* (Blanchard, 1836) (India)
				Stibarosterna serrata Uvarov, 1953 (Angola)
				Tenuitarsus angustus (Blanchard, 1836) (Mauritania)
			Pyrgomorphini	*Afrosphenella capensis* (Key, 1937) (South Africa)
				Chirindites odendaali Ramme, 1929 (Zimbabwe)
				Parasphena imatongensis Rehn, 1942 (Sudan)
				Parasphenella dubia (Bolívar, 1904) (Kenya)
				Parasphenula yemenita (Uvarov, 1936) (Yemen)

Table 6.2. Continued

Family	Subfamily/Group	Series	Tribe	Species
				Pezotagasta bredoi Dirsh, 1961 (Democratic Republic of the Congo)
				Stenoscepa gracilis (Kevan, 1956) (Zimbabwe)
				Anarchita aptera (Bolívar, 1902) (India)
				Laufferia chloronata (Bolívar, 1889) (Angola)
				Leptea debilis (Finot, 1894) (Algeria)
				Ochrophlebia cafra (Linnaeus, 1764) (South Africa)
				Ochrophlegma pygmaea (Karsch, 1888) Mozambique
				Phymella capensis Uvarov, 1922 (South Africa)
				Plerisca rubripennulis (Key, 1937) (South Africa)
				Protanita fusiformis (Sjöstedt, 1929) (Tanzania)
				Pyrgomorpha vignaudii (Guérin-Méneville, 1847) (Ethiopia)
				Pyrgomorphella arachidis Dirsh, 1951 (Tanzania)
				Pyrgomorphellula curtula (Uvarov, 1952) (Yemen)
				Scabropyrgus scabrosus (Bolívar, 1889) (Angola)
				Tanita parva Kevan, 1962 (Tanzania)
				Zarytes squalinus (Saussure, 1884) (India)

6.2.3 Dissection methods

I followed the same general dissection methods described in Chapter 4. New to this study was the dissection of female spermatheca. This was done by removing the subgenital plate together with the valves of ovipositor. Dissected female genitalia were placed in 10% KOH for maximum 10 minutes to dissolve muscle tissues. Both subgenital plate and valves with spermathecal were placed in vials with ethanol 70%.

6.2.4 Digital imaging and illustration

I followed the same general imaging methods described in Chapter 4. In addition to the images of males, I also included the photographs of females when available both in dorsal and lateral views.

6.2.5 Cladistic analysis

A data matrix consisting of 113 terminals (8 outgroups and 105 ingroups) and 149 characters with 338 character states was compiled in WinClada (Nixon, 2002). Non-applicable data were recorded as "-" and missing data as "?". 108 characters were neomorphic and 41 transformational (Sereno, 2007). For the uninformative states, I atomized the characters using contingent coding (Brazeau, 2011). All the characters were coded non-additively and equally weighted. The data matrix used in this analysis is presented in Table 6.3. The data matrix was exported and submitted to TNT (Goloboff et al., 2003) using a combination of sectorial search, drifting, tree fusing (Goloboff, 1999), and ratchet (Nixon, 1999). Bremer support

Table 6.3. Matrix.

Prionotropis	0000020-00-0101010010001----11111-12111102101102220000012020 2-022100011--000100001000001000000 1-00000000001110--1100110000-0000000000000-0000111011110
Lentula	0200020-00-0101010010011----00-11-01100100001100100011210010 0-00011000-----------0-000010000001000000000001110--1000110000-0000000000000-0201111001--0
Guaranacris	1100000100-0100-0-010011-0-110-11-11101100101110100021201010 0-011100011--000001001100001001000102000000011110--1100110000-0000000000000-02111110*1111
Trigonopteryx	2211000200201110100 0-010-0-11110-01111110000010010001120000 100-011100011--000100001000011000000 0-000-000-00--10--1100100000-0000000000000-01-0000001000
Locusta	0000010-00-00-0-0-010000-0--1110--11101002100020000021210010 0-011100011--000101001000011000000100000000001110--1100110000-0000000000000-02111110*1111
Physemacris	0000020-00-0110-0-00-010-0--11111-12101002000110100001000010 0-011100011--000101001000011000000 0-000-000-00--10--1000100000-0000000000000-01-0000--0--0
Pyrgacris	2200002000200010100 0-01000-01110--0011000001-1-0100001200010 0-00001000-----------0-000010000000-000000000011110--1100110000-0000000000000-02-11110???00
Tanaocerus	2200011000201010100100000 0-01110-01100100000-1-0100021000010 0-01110000-----------0-000110000000-000-000-00--10--1000100000-0000000000000-01-0000--0--0
Chapmanacris	2210002000001010100110100 0-01110-00010000000000100001100000 0-00011000-----------0-111000000010100000000111100121010000000100000000100102-00011-1--0
Pseudogeloius	2200102110201010100110110110011100-100101000000002200010100002-00011000-----------0-101301000010100000000111111111010000000000000000100102-00011-1--0
Gymnohippus	2101020010201111110100100101 00-11100100000011002120010110 0001-00111000-----------0-001101000010100010000112001 0-100000000000000000010010102-00011-1--0
Sphenacris	2101100100201111110100110 0-11111110010100000101222000111001 00-02211000-----------0-000211000010100000000111110121001000000100000000100102-00011-1--0
Mitricephala	2200000000201010100110110 0-100-101011000001010001000011000 100-000110011--0-------111010011000101000000001111101210100000001000000011000102-00011-1--0
Modernacris	220001000020110-0-01001100-000-11100110000000000100011200010 0-00011100-----------0-101001100010100000000111011010200000000010001000000002112-00011-1--0
Acropyrgus	2101111000001111 0-01001100-110-11100110000002010100020210000 0-01111000-----------0-000211000010100000000111111121000000000100000000100102-00011-1--0
Caprorhinus	2111102100201010110011010111111201100000000001000011100100 0-01111001001--------0-001100000010100000000111111121000000000100000000100102-00011-1--0
Orthacris	2201010000200-0-0-01001101011110-10010000000000010001111000000 0-00011000-----------0-000111000010100000000111111121000000000100000000100102-00011-1--0
Colemania	2210002200200-101001000100-11111012010000000000000000011010100 0-00011001020--------0-000101001110100010000111111121001000000100000000100102-00011-1--0
Acanthopyrgus	2210002010201010100100110 0-11111010010000001010100111210010 0-00111000-----------0-000101000010100010000110111212001000000000000000100002 02-00011-1--0
Meubelia	2200010000201010100 0-01100-01110-00010000000111010002120000 100-00011001011--------0-001200000010100010000111100100001000002110000010010 0102-00011-1--0
Atractomorpha	2010000100201111101110 0100-11111111110110010111020002121100000 0-01110011--0010010011000111000010100001001111101210000000001000100001130 2502-00011-1--0
Chlorizeina	2110010000201010100100010101111111111111000011000000011110100 0-01111001 1--0010010011001121000010101000000111110121000000000100011000012012102-00011-1--0
Humpatella	2201010000201110100110010101111111111100000100100000021111010 0-01111001010--------0-001121000010101000000111111121000000000100011000012012102-00011-1--0
Chrotogonus	2100010001201111110110010111111111111111011111112220020111010 0-00101001 1--0010011010000201000010110100000111110121000000000100000000100102-00011-1--0
Tenuitarsus	2100011001201010110110010111111111111111011101122200202100100 0-00000011 1--0010011010001201000010110100000111110121000000000100000000100102-00011-1--0
Desmopterella	2210001000201010100100110101111111111010010021010000111000 0-01111001 1--0000010010000101000010100000000111110121001000110100010000010121 02-00011-1--0
Dictyophorus	2001120100210-0-0-01100100-11110-11111000210212303002101111 1-1011100011--000110001100020000011010000000011111012100000000010011011010002302-00011-1--0
Ichthyotettix	2200011000201111101100110111111111100101000101002020001010010 0-01111000-----------0-1010?100001010000001011111012000000000100000000110001 02-00011-1--0
Monistria	2011110000201010100100010101111111111101000002120000021010111 0-0111001 1--1001000011000200000110100000000101110111001000000100000000000002102-00011-1--0
Omura	2010002300201010100100100 0-11110-12011110010212020001101100 00-01110000-----------0-000110000010100000000111110121000000001100001000100006 02-00011-1--0
Petasida	2201020100200-0-0-01100101011111111120-10021121201000110111 1-0011000011--000110001100020000011010000000011110111001000000100010000000002102-00011-1--0
Phymateus	2201020100200-0-0-01110111011111111111010011011010100110111 11-0011100011--000101001100010000111010000100011111012100000000010000100012000102-00011-1--0
Zonocerus	2201020000200-0-0-01110110-11111111110100010010000011011111-0000100011--000101011100010000111010000100011111011100100000010000100012000102-00011-1--0
Poekilocerus	2201010000201010100110011101111111111101001101100100001011111-0011100011--000101001100010000111010000100011111012100100000010000100012000102-00011-1--0
Psedna	2010102100201010100110110110111110-00010100000-1?000100101001001 00-11000010100100-10010000010--------0-001011010010100000000101111011100000001000000001100002-00011-1--0
Psednura	2010102100201010100111010111110-00010100000-1?000100101001001 00-11000010100100-10010000-----------0-001011010010100000000101111101000001000100000000011000 02-00011-1--0
Pseudomorphacris	2100001000000-10101110110101111 0-11111100010211010001101100 00-01110000-----------0-011001001000111100001010000000111111011101000000010000000011200102-00011-1--0
Anarchita	2100102000201010110011011110-11010111100000100100000011010 0-01100000-----------0-000111000010110100000111110121000000000100000001001000602-00011-1--0
Parasphena	2101111000200-10101100010111111111111111001111101000110110100-01110000-----------0-000111000010110100000111110121000000000100000001000000602-00011-1--0
Pyrgomorpha	2100000100201010101110010111111111111101100101110100011011 0000-01100011--001001001000011000001011010000011110012100000000010000001001000602-00011-1--0
Zarytes	2000102000201010101100110111111111110111100101110100011011 0000-01100011--001001--1000011100001010000000111110012100000000010000001001000602-00011-1--0
Schulthessia	2110002000001010101100110101111111111111001121202000212110000 0-01110201 1--0010010010000110000010110100000111100121000000000100010100110021 02-00011-1--0
Mekongiana	2201020000201010100110010101111111111101100101110100021011 0100-01110000-----------0-000210000010100100000111110121001000000100000000000602-00011-1--0
Prosphena	2001000200101010110001010111111111111011001020201000110110100 0-01110001020--------0-000210000010100100000111110121001000000100000000011010602-00011-1--0
Rubellia	2201000100201010100100010101111111111101100101110000021011010 0-01110001 1--1001010011000211000010100100000111110121000000000100000001000602-00011-1--0
Sphenarium	2201001100101010100100110101111111111101100102010000021011010 0-01110001020--------0-000211000010100100000111100121001000000100000000011010602-00011-1--0
Tagasta	2210000000001010101100010101111111111101100101110100021211000 0-01110001 1--0110010011000111000010101000000111110121000000000100001000001200402-00011-1--0
Aularches	2201020000200-0-0-00-00100-11110-1110-10011011110300010111 11-0001100011--000110001100010000011011000000011111012100000000010001010010002102-00011-1--0
Taphronota	2101000000200-100-01100100-11110-01110100110111200000101111 1-0011100011--000100001100010000010101?000000011111112100100000010001000010002102-00011-1--0
Afrosphenella	2110102000201010110100110111111111111101100111110100021011000 0-01110001010--------0-000111000010110000000111110012100000000010000000100000602-00011-1--0
Algete	2010102200201010110011011111111002010110010200010000121100 00-01110000-----------0-000120000010100000000111110121000000001100001000100006 02-00011-1--0
Ambositracris	2201101000201010100100110101111111100111000101000100011010 0100-01111000-----------0-000110000110100000000111111121000000000100000000100001 02-00011-1--0
Annandalea	2210000000200-1010010001010111111111110110010111001000211010100-00010001 1--0010010011000111000010100000000111110121000000000100001000001200402-00011-1--0
Apodesmoptera	2210000000201010100100110101111111111101000002120100021100000 0-01110001 1--0000010010000101000010100000000111110121001000011010001000000012102-00011-1--0
Brunniella	2010002000201010100100110101111111011101100001110100001210010 0-111100011--0100011010000020010010100020000101110121000001000100000000000001102-00011-1--0
Burmorthacris	2200000000201010100100010101111111101100000000120100011010000 0-01110001000--------0-000111000010100000000111111121000000000100001000100002 02-00011-1--0
Calamacris	2010101000201111111110011010111111120101100001122220001211010 0-00101100001--0010011000010100000000111110121001000000100000000001000102-00011-1--0

Table 6.3. Continued

Camoensia	2001120100210-0-0-01100100-11110-11111110011021230300001011111-0011100011--0001100-11000200000110100000000011111012100000000010011011010002302-00011-1--0
Cawendia	2200010000201010100100010101111111111101000100120100021110010 0-01111001010--------0-0011100000101010000001111111210000000001000110001201210 2-00011-1--0
Chirindites	2100000100201011100100010101111111111101000101112220021012000 0-01210001020--------0-0001100000101000000001111101210010000001000000100000060 2-00011-1--0
Desmoptera	2110000000201010100100110101111111111101000002120100021110000 0-01110011--0000010010000111000010100000000111110121001000110100010000000121 02-00011-1--0
Dyscolorhinus	2201101000201010100100110101111111100111000100000100011010010 0-01111000-----------0-0001110001101000000001111111210000000001000000001000010 2-00011-1--0
Greyacris	2201010000211010100100100-11111111111000010211222001101011 1-0011100011--000??000110002200001101000000001011101110010000001000000000002102-00011-1--0
Ichthiacris	2201001000201010100100110111111111110000100010000100001100100-01111000-----------0-0001110000101000000001111101210010000001000000000001000102-00011-1--0
Jaragua	2010102200201010101100110111111100111111100102020100021211000 0-01110001010--------0-0001100000101000000001111101210000000011000010001000602-00011-1--0
Laufferia	2000110000201010101100010111111111111011001011001000110100000-011100011--0010010011000010000110110100000111110121000000000100000001001000102-00011-1--0
Leptea	2100100000201010101100111011110-11100101000102010100001011010 0-01110001010--------0-0001100000101101000001111100121000000000100000001000102-00011-1--0
Loveridgacris	2001120200210-0-0-01100100-11111111110100110212323001101110 1-0011100011--0001100011000211000110100000000111110121000000000100110110100023 02-00011-1--0
Maura	200112000021 0-100-01100000-11111101111100110212323001101010 1-0011100011--1001100011000211000110100000000111110121000000000100110110100023 02-00011-1--0
Menesesia	2100000000201010100100110101111111111101000002122220011110000-011100011--0000010010000110000010100000000111110121001000110100010000000121 02-00011-1--0
Menesesiella	2100000000201010100100110101111111111101000002122220011110000-011100011--0000010010000110000010100000000111110121001000110100010000000121 02-00011-1--0
Minorissa	2010002200201010101100110101111101111111100102020100021211000 0-01110001010--------0-0001100000101100000101000000011111012100000000110000100010000602-00011-1--0
Neorthacris	2201101000201010100110101111101001000000000010000110000-01111000-----------0-0001110000101000000001111101210000000001000000001000102-00011-1--0
Nerenia	2000100000201010100100110111111110000011100010110010002121001 00-01111000-----------0-0011111000101000100001101101020000000001000100000001210 2-00011-1--0
Nilgiracris	2001102000201010100100110111111110100111000101100100021110010 0-01110000-----------0-0001100000101000100001111112100100000001000000001000102-00011-1--0
Occidentosphena	2101111000201010101100010111111111111010001011101000212110000 0-01110000-----------0-0011110000101000001001111112100000000010001000011302502-00011-1--0
Ochrophlebia	2101110000201011100100010111111111111111000101122200021011010 0-01110001100-0010010011000110000110110100000111110121000000000100000001001000602-00011-1--0
Ochrophlegma	2101100000201011101100010111111111111111000101122200021011010 0-01110001100-0010010011000110000110110100000111110121000000000100000001001000602-00011-1--0
Parapetasia	200112020021 0-0-0-01100100-11111011110100110212323001100010 1-0011100010100--------0-0002110000101000000001111101210000000001001101101000230 2-00011-1--0
Paraphymateus	2201020000201 00-1001000110-11111111111100010100310000101111 1-0011100011--000???0-1100021000111010000100011111012100000000010000100012000102-00011-1--0
Parasphenella	2201100000201010110011001101111111111101011100101100100021010010 0-01110001020--------0-0001100000101101000001111101210000000001000000100000602-00011-1--0
Parasphenula	2201100000201010101100110111111111101011001011001000210120000 0-01110001020--------0-0001100000101101000001111101210000000001000000100000602-00011-1--0
Paratarbaleus	2100020000201110 0-01001100-01111110011000000012010001120000100-00011100-----------0-0001110000101000000001101101020000000001000100000002202-00011-1--0
Pezotagasta	2001000102010101011001101111111111101111000100100100021010000 0-01110001--0010010-1100011000001011010000011111012100000000010000001000000602-00011-1--0
Phymella	2001110000201111111100010111111111011110000021222200210120000 0-01110001--0010010011000110000010110100000111110121000000000100000001001000602-00011-1--0
Physemophorus	2001020000201010100110110-11111111111100000000010001101011 1-0000110011--0001010011000110001010100000000111110111001000000100001000120 02-00011-1--0
Phyteumas	2201020000201010100100110-11111111111010001011011102101111 1-0011100011--0001010011000110001110100001000111110121000000000100001000120 02-00011-1--0
Piscacris	2201001000201111110100110111111111100101000101002020001010010 0-01110000-----------0-1000?100001010000000011111012000000000010000000011000102-00011-1--0
Plerisca	2101100000201010101100110111111111101111000101110100021112000 0-01110001--0010010-1100011100001011010000011110012100000000010000001001000602-00011-1--0
Popovia	2201001000201010100100110111111111111001010000000010000101001 00-00011001010-------0-0011100000101000100001111111210010000001000000001000102-00011-1--0
Propsednura	2011102100201010100100110110111 0-00010100000-1?000100101001 00-10010001010--------0-0010110100101000000001011101110000001000100000000011000 02-00011-1--0
Protanita	2101101200201010101100110101111111111010000011001000110110000 0-01110001--0110010011000111000110110100000111110121000000000100000001001000602-00011-1--0
Pterorthacris	2201010000201010 0-01000100-11111110110000000012010001101001 00-00100011--0010010011001021000010101000001111101210000000001000011000120 02-00011-1--0
Pyrgohippus	2000110010201111110100110101111101001100000000022000212100000 0-01110000-----------0-0001110000101000000001120010-10000000000000000000010010102-00011-1--0
Pyrgomorphella	2101101100201010101100110111111111110111100101110100011011000 0-01110001--0010010-1100111000001011010000011111012100000000010000001001000602-00011-1--0
Pyrgomorphellula	2000100000201010101100110111111111110111100102010100011010000 0-01110001000--------0-0001100000101100000111110121000000000100000001001000602-00011-1--0
Pyrgotettix	2201010000200-0-0-01001101011111101001010001000000000010100100-01111000-----------0-0000110000101000000001111101200000000001000000001100010 2-00011-1--0
Rutidoderes	2201020000201010 0-01100110-11111111111010001010011100010101 1-0011110011--0001010011000211001110100001000111110121000000000100001000120 02-00011-1--0
Scabropyrgus	2101100000201111111100110111111111111100102102220021010000 0-01110001--0010010011000110000010110100000111110121000000000100000001001000602-00011-1--0
Sphenexia	2011000200201010100110100-11111111110100010210010002101200 0-01110001--001???0-1?0002100000101100000001111101210010000001000000000000102-00011-1--0
Sphenotettix	2201101000201010100110101111111111001010001011001000010100000-01111000-----------0-0001200000101000000001111101200000000001000000001100010 2-00011-1--0
Spinacris	2200010000201010100-01100-01111110110000010111010002120001 00-000112011--0010010010000110000010100010000111100100001000000211000001001001 02-00011-1--0
Stenoscepa	2001100100201010101110110111111111111110100010110010001111200 0-01110001020--------0-0001110000101101000001111101210000000001000000010000060 2-00011-1--0
Stenoxyphus	2200000000201010100100110101111111111101000001122200021110000 0-01110001--0000010010000110000010100000000111110121001000110100010000000121 02-00011-1--0
Stibarosterna	2200110001201110110110010111111111101110101021022001101000 0-01100000-----------0-0002100000101101000001111101210000000001000000001001010 2-00011-1--0
Tanita	2100101000201111111110101111111111111111100101102220011111000 0-01110001--0110010011000110000110110100000111110012100000000010000001001000602-00011-1--0
Tarbaleopsis	2200020000201111110100010-01111111001000000002222000212100100-00011000-----------0-0001110000101000000001101101020000000001000100000002102-00011-1--0
Vittisphena	2101100000201010100110110111111111101010000010001000010100100-01110000-----------0-0001110001101000000001111111210000000001000000001000102-00011-1--0
Xenephias	2010101100201010100110110101111110101010001010101000110100000-01110000-----------0-0001100000101101000001111101210010000001000000000000102-00011-1--0
Xiphipyrgus	2000101100201010101110110111111111101101111100102100100?10100000-01110001--00?0010010000111000001 01?????????1?????????0??000000100000001000000102-00011-1--0
Yeelanna	2001020000201010100110110101111111110-10001021101000?1110111-0011100011--000???0-1100021000011010000000010111011100100000010000000000002102-00011-1--0
Yunnanites	2201110100201010101100110111111111111111000101002220011111000 0-01110001020--------0-0001100000101000000001111101210010000001000000000000602-00011-1--0
Geloius	2000101210201010100110110 0-11111110011100010000010001010010 0-01110001020--------0-0010100000101000000001111111110100000000000000000000102-00011-1--0

values (Bremer 1994) were calculated up to five by thoroughly searching suboptimal trees five steps longer in TNT.

6.3 Results

6.3.1 Phylogenetic analysis

The analysis resulted in 446 equally parsimonious trees of 1152 steps with the consistency index (CI) of 0.16 and retention index (RI) of 0.60. A strict consensus collapsed 53 nodes and included numerous polytomies, but the following relationships were unaffected by this method: tribes Psednurini, Chlorizeini, Gymnohippini, Verdulini, Desmopterini, Monistriini, Dictyophorini, Atractomorphini, Tagastini, and Chrotogonini (fig. 6.16). The following discussion about the relationships is based on one of the most parsimonious trees selected as a preferred tree in fig. 6.11-6.15.

I recovered the family Pyrgomorphidae as a monophyletic group, but the groups A and B *sensu* Kevan were not recovered as monophyletic groups. Similarly, none of the 10 series that Kevan recognized was recovered as monophyletic. Of the 29 tribes included in the analyses, 8 tribes were monotypic so I could not test monophyly, but 21 tribes had at least two taxa included in the analysis. Regarding these 21 tribes, 10 tribes were found to be monophyletic (Psednurini, Chlorizeini, Gymnohippini, Verdulini, Desmopterini, Monistriini, Dictyophorini, Atractomorphini, Tagastini, Chrotogonini), while 11 were shown to be paraphyletic (Geloiini, Ichthiacridini, Ichthyotettigini, Orthacridini, Popoviini, Nereniini, Phymateini, Sphenariini, Taphronotini, Omurini, Pyrgomorphini).

Within Pyrgomorphidae, three main clades were recovered (fig. 6.11-6.14). Because less than 50% of non-monotypic tribes were monophyletic based on this morphological dataset, it is

unnecessary to keep using Kevan's tribe names. I do not attempt to rename the clades or modify tribe concepts. The following section is simply based on the topology and includes the discussion of the three major clades. The first clade represents the earliest diverging lineage within Pyrgomorphidae and consists of *Brunniella* and the three Australian endemic genera *Psedna, Psednura,* and *Propsednura* (fig. 6.12). The second clade consists of 35 genera, many of which can be characterized by elongated and cylindrical body forms. One of the subclades within this clade consists of seven genera distributed in Mexico, often referred to as Ichthiacridini and Ichthyotettigini, which were discussed in Chapter 5 in detail. Most relationships within this clade vary across the 446 equally parsimonious trees so that the strict consensus renders most relationships to be unresolved (fig. 6.13). The third clade consists the remaining 66 genera that include all of the large and colorful pyrgomorphs, such as *Phymateus*, *Poekilocerus*, and *Dictyophorus,* and robust and cryptic genera such as *Atractomorpha* and *Pyrgomorpha*, mostly distributed in Africa and Asia. It also includes two separate subclades of the New World genera, (*Sphenarium* + *Prosphena*) and (*Minorissa* (*Jaragua* (*Omura* + *Algete*))). Unlike the weakly supported groups within the second clade, the majority of the relationships within this third clade were consistently recovered across all equally parsimonious trees (figs. 6.14-6.15).

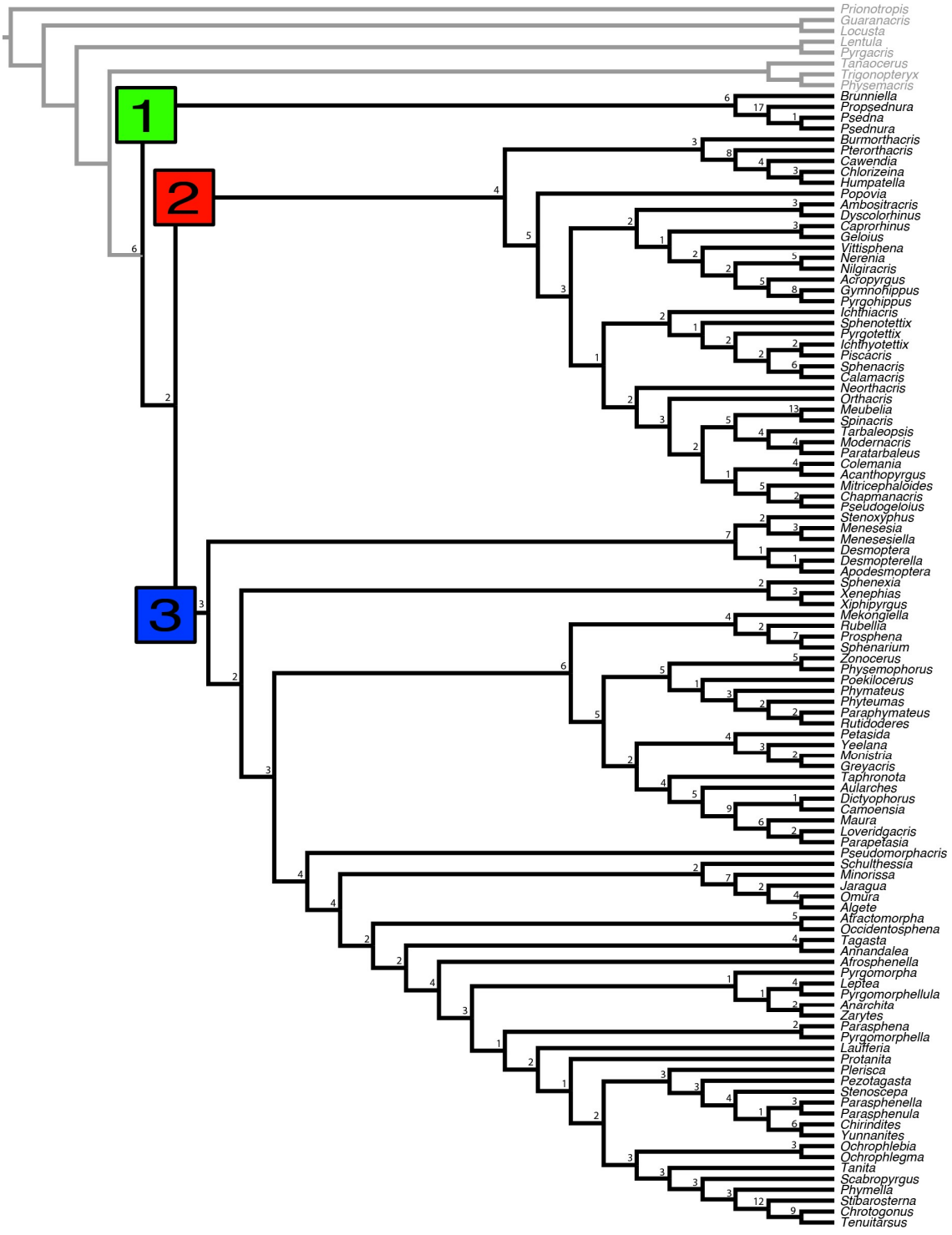

Figure 6.11. One of the most parsimonious trees presented here as a preferred tree. L = 1152, CI = 16, RI = 60 with the three main clades identified. Number of synapomorphies for each clade is indicated.

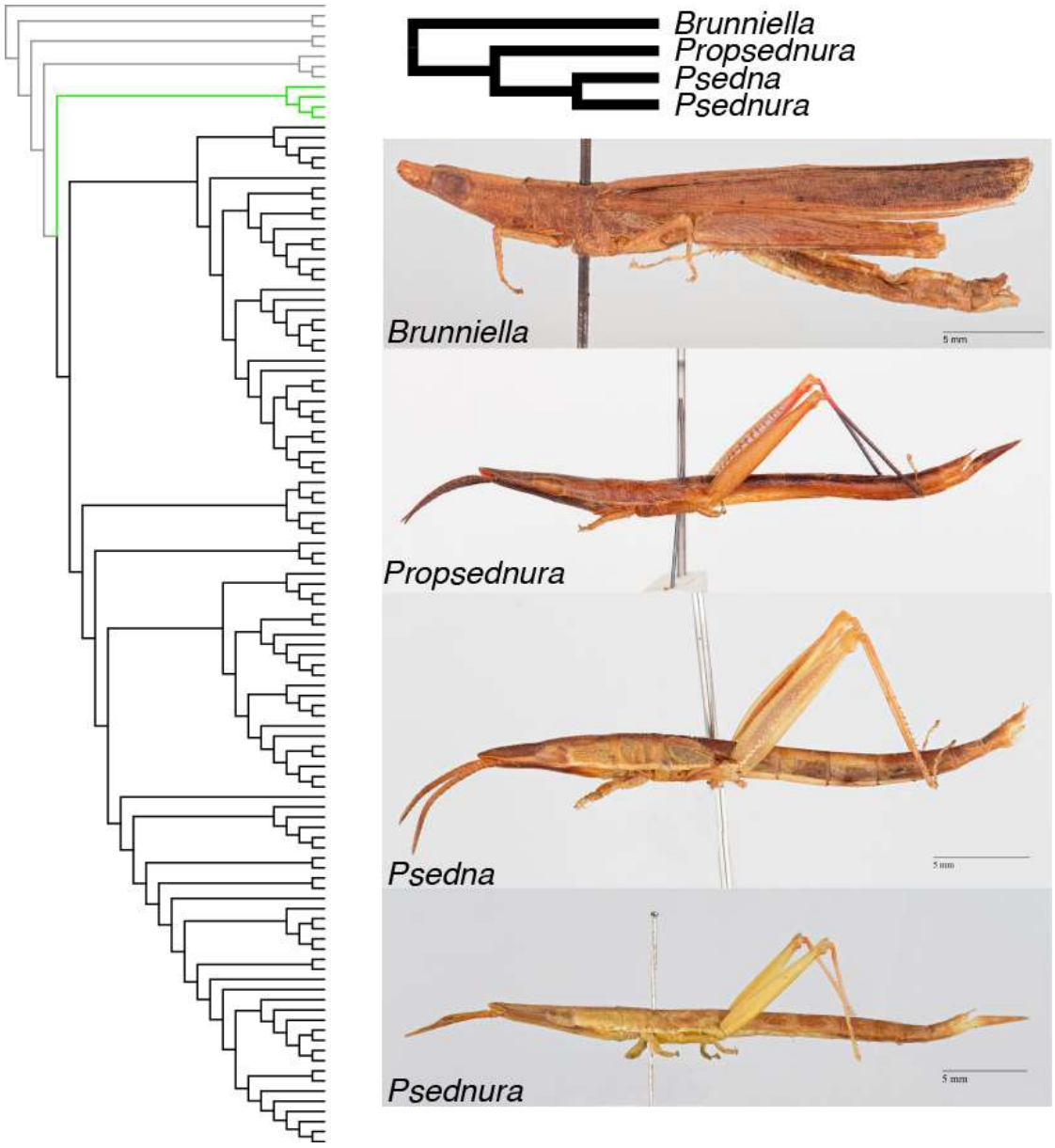

Figure 6.12. Detail of clade 1 of the preferred most parsimonious tree.

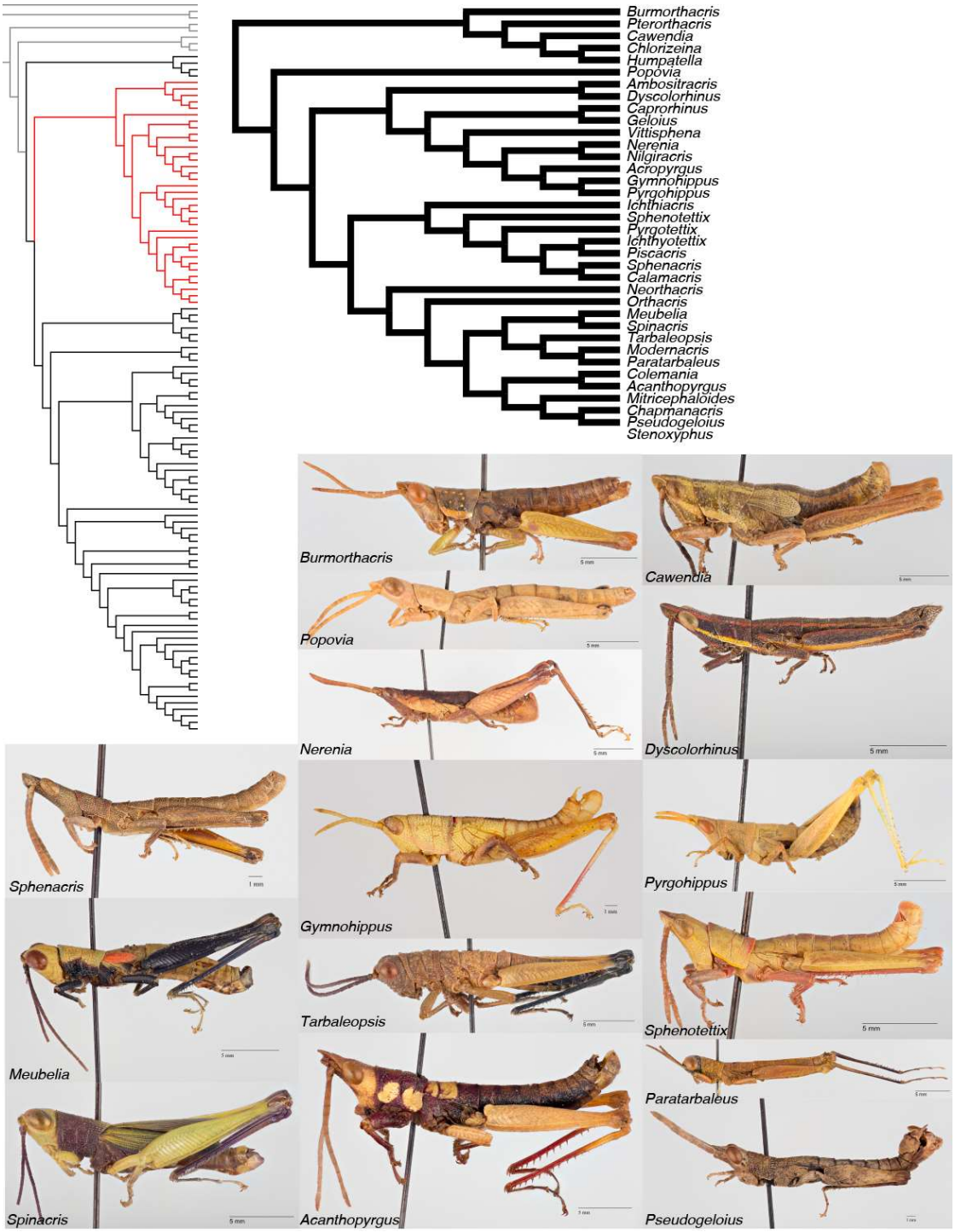

Figure 6.13. Detail of clade 2 of the preferred most parsimonious tree.

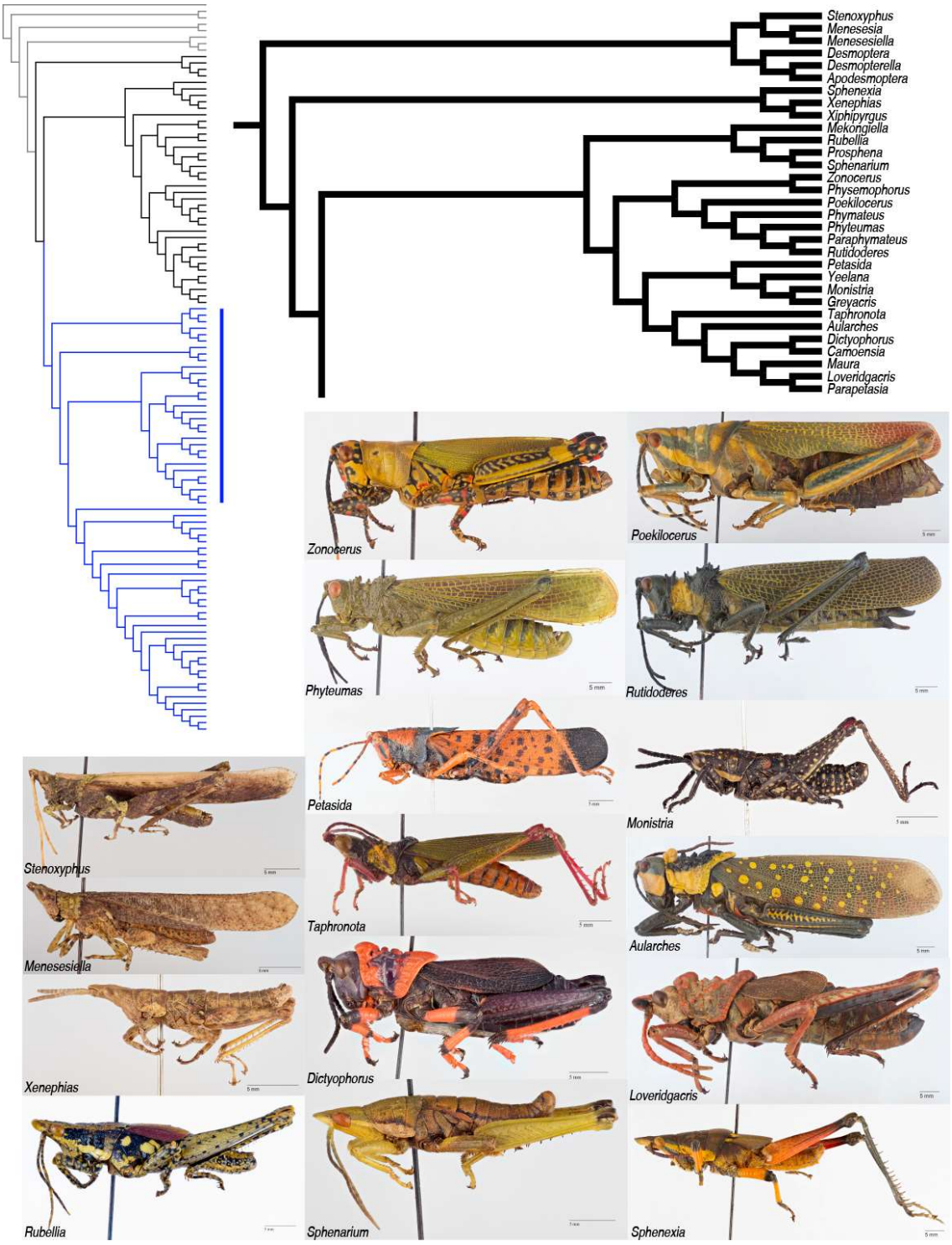

Figure 6.14. Detail of clade 3 (first part) of the preferred most parsimonious tree.

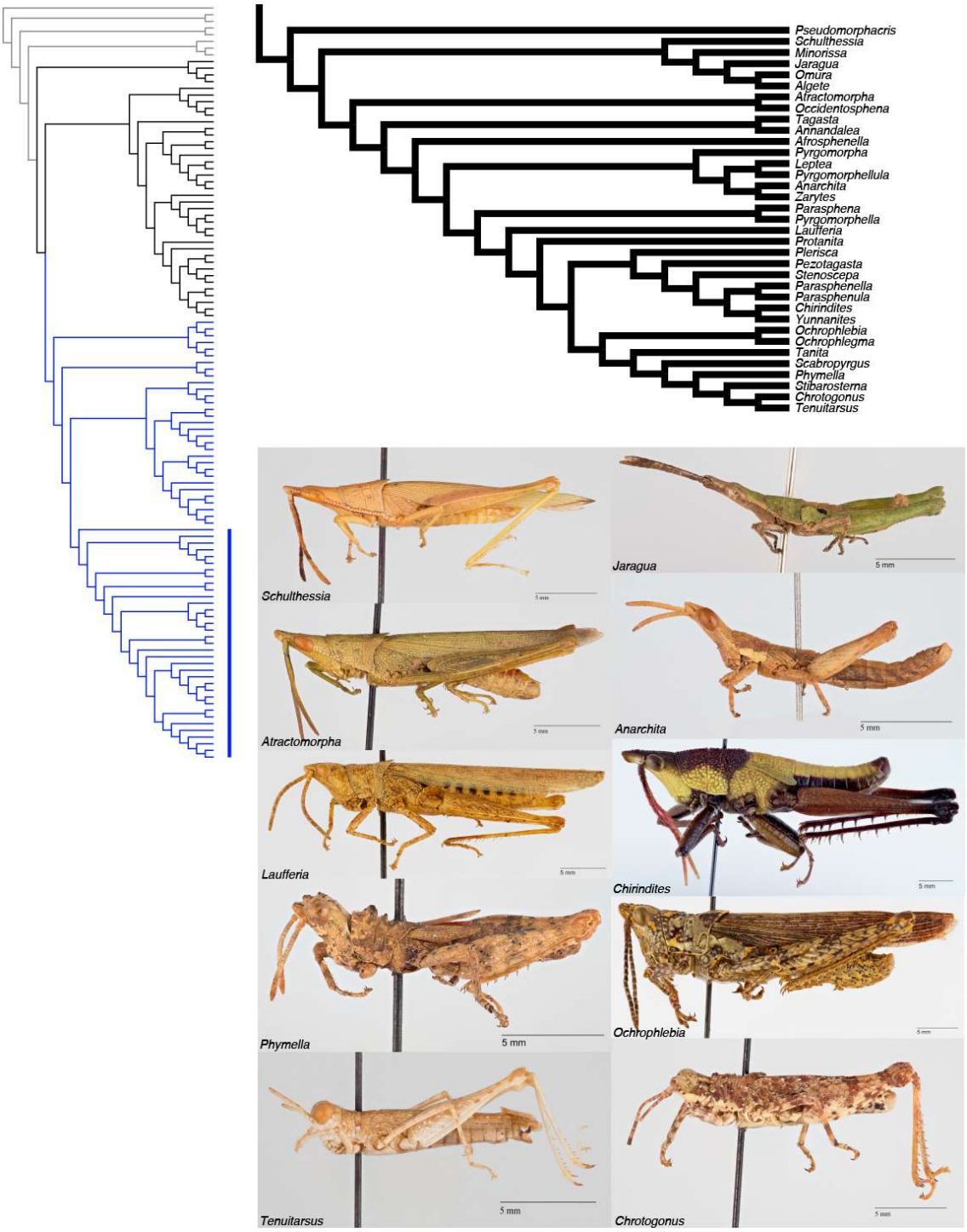

Figure 6.15 Detail of clade 3 (second part) of the preferred most parsimonious tree.

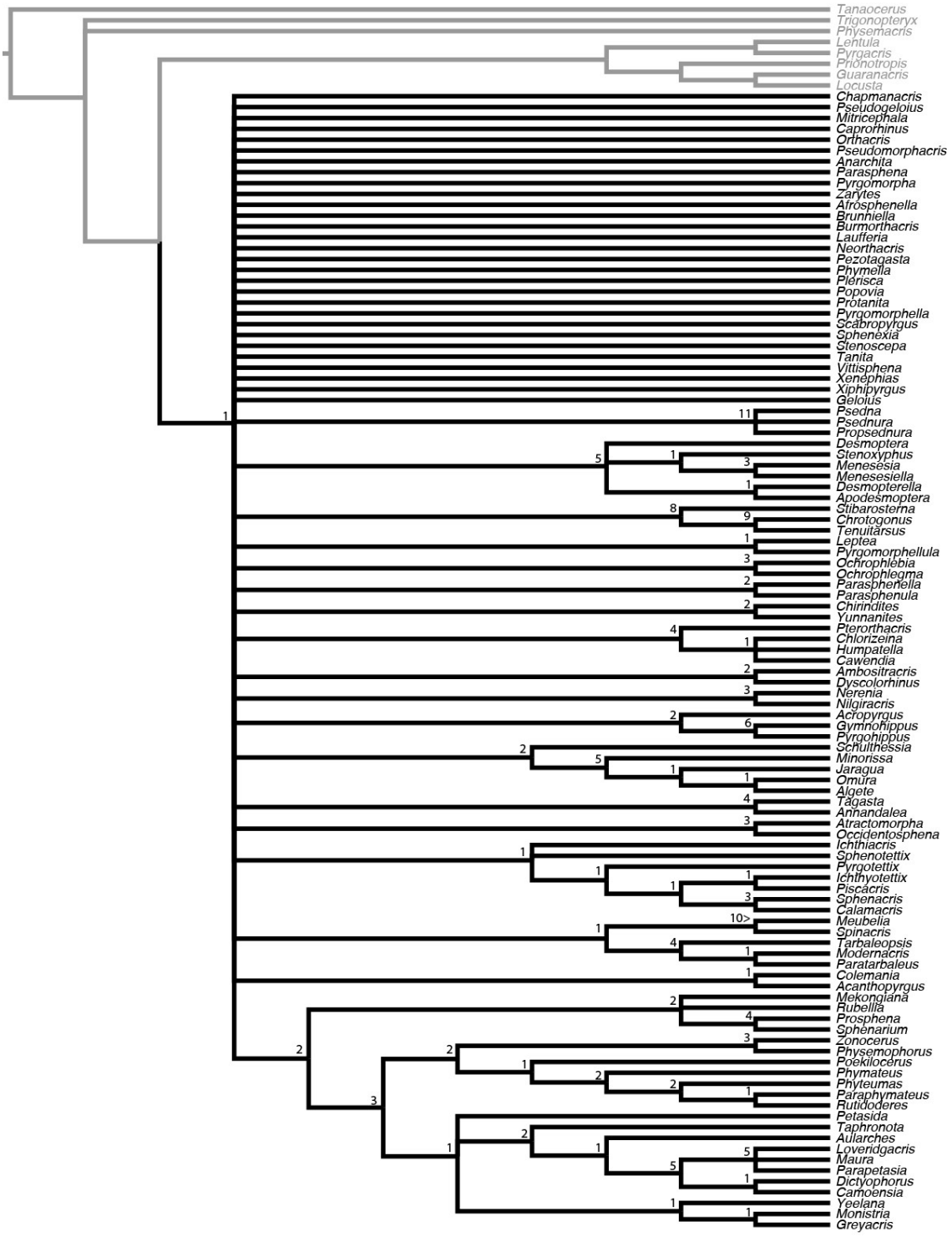

Figure 6.16. Strict consensus tree of 446 equally parsimonious trees. Numbers indicated Bremer support values.

6.3.2 Description of new characters, including comments on character optimizations

In Chapter 4, detailed descriptions of 117 characters used in the phylogenetic analysis were already presented. The 12 characters taken from Song and Mariño-Pérez (2013) mostly differentiate among the outgroup taxa. Thus, here I only comment about the 20 new characters pertinent to the Pyrgomorphidae relationships. In general, they had high CI and RI values, and their phylogenetic signal helped to resolve some relationships. Several characters are synapomorphies for the 10 monophyletic tribes (Psednurini, Chlorizeini, Gymnohippini, Verdulini, Desmopterini, Monistriini, Dictyophorini, Atractomorphini, Tagastini, Chrotogonini), and the utility of these characters are discussed in reference to these tribe names.

118. Galeae of the maxillae, condition: (0) normal, (1) turn forward over the labrum. CI = 100, RI = 100. The galeae in the majority of Pyrgomorphidae are normal but in the clade composed of *Brunniella, Psedna, Psednura* and *Propsednura,* the galeae are turned forward over the labrum (Kevan et al., 1970). This structure is also reported in *Fijipyrgus*, but unfortunately I was not able to obtain a specimen.

119. Body, lateral compression: (0) absent, (1) present. CI = 100, RI = 100. The body compressed laterally is an uncontroverted synapomorphy uniting a clade consisting of *Apodesmoptera*, *Desmoptera*, *Desmopterella*, *Menesesia*, *Menesesiella*, and *Stenoxyphus* (Kevan et al., 1972).

120. Tegmina, sided parallel: (0) absent, (1) present. CI = 100, RI = 100. Members of tribe Desmopterini (*Apodesmoptera*, *Desmoptera*, *Desmopterella*, *Menesesia*, *Menesesiella*, and *Stenoxyphus*) possess this condition in tegmina with an exception of a species in the genus *Apodesmoptera* that has reduced tegmina (Kevan et al., 1972). It is an uncontroverted synapomorphy of this clade.

121. Fastigium, condition: (0) not interrupted by eye, (1) interrupted by eye. CI = 100, RI = 100. The members of the South American genera *Omura*, *Algete* and *Minorissa*, together with the Caribbean genus *Jaragua* have the eye interrupting the fastigium of vertex. It is an uncontroverted synapomorphy for the clade consisting of these four genera.

122. Basal emargination of cingulum, depth: (0) shallow, (1) normal, (2) deep. CI = 40, RI = 40. The great majority of Pyrgomorphidae have a normal depth of the basal emargination of cingulum. In four cases, it has evolved independently to be shallow, in all cases in the Madagascar genera. The deep condition has evolved once in the clade comprised of *Meubelia* and *Spinacris*.

123. Valves of cingulum, size: (0) normal, (1) large. CI = 100, RI = 100. All Pyrgomorphidae except *Meubelia* and *Spinacris* possess normal valves of cingulum. The condition to large valves has evolved once in this clade.

124. Valves of aedagus, size: (0) normal, (1) large. CI = 100, RI = 100. All Pyrgomorphidae except *Meubelia* and *Spinacris* possess normal valves of aedagus. The condition to large valves evolves once, in this clade.

125. Ovipositor valves, size: (0) normal, (1) large. CI = 100, RI = 100. In general the size of female valvae is normal and easy observable to the naked eye. This structure has been reduced in all the known genera of the clade consisted of *Dictyophorus, Camoensia, Maura, Loveridgacris, Parapetasia*. In these cases, it is extremely difficult to observe the female valvae and only because of the size it is possible to differentiate between males and females.

126. Apical bulb of spermathecal appendage, condition: (0) absent, (1) present. CI = 12, RI = 70. The absence of this bulb is the ancestral condition. The apical bulb has evolved seven independent times (ACCTRAN).

127. Apical pocket of spermatheca, condition: (0) absent, (1) present. CI = 25, RI = 81. The evolution of apical pocket has occurred four independent times.

128. Secondary diverticulum of spermathecal appendage, condition: (0) absent, (1) present. CI = 50, RI = 83. This character has evolved twice.

129. Valvae of spermathecal duct, condition: (0) absent, (1) present. CI = 25, RI = 88. This valvae has evolved two independent times.

130. Sclerotized ornamentation of postvaginal sclerite, condition: (0) absent, (1) present. CI = 100, RI = 100. The general condition in Pyrgomorphidae except *Meubelia* and *Spinacris* is an unsclerotized postvaginal sclerite. The sclerotization has evolved only in this clade.

131. Posterior edge of subgenital plate condition: (0) smooth, (1) serrated. CI = 8, RI = 79. The serrated subgenital plate evolved multiple times across the family.

132. Columellae, condition: (0) absent, (1) present, (2) columellae-like thickenings. CI = 15, RI = 74. The ancestral condition is the absence of columellae with several independent gains throughout the phylogeny.

133. Terminal dilation of spermathecal duct, condition: (0) normal, (1) dilated, (2) short and prominent, (3) large and prominent. CI = 60, RI = 71. There were two independent events to a dilated terminal of spermathecal duct in the clade consisted of *Psedna, Psednura, Propsednura* and the clade composed of *Meubelia* and *Spinacris*. There was also a transformation to short and prominent in the clade consisted of *Tagasta* and *Annandalea* and to large and prominent in the clade composed of *Atractomorpha* and *Occidentosphena*.

134. Spermathecal duct, condition: (0) simple, (1) long. CI = 12, RI = 63. There have been eight independent transformations to a longer spermathecal duct.

135. Spermathecal appendage, condition: (0) absent, (1) subterminal, (2) terminal. CI = 25, RI = 77. Usually this appendage is absent. In *Brunniella* it is subterminal and it has evolved to the terminal condition seven independent times.

136. Caecum of spermatheca, condition: (0) absent, (1) simple, (2) enlarged, (3) complex, (4) thick, (5) long (bifid), (6) long. CI = 50, RI = 83. The ancestral condition was a simple spermathecal caecum with a loss in the clade consisted of *Psedna*, *Psednura* and *Propsednura*. Its various conditions have evolved multiple times throughout the phylogeny.

137. Spermathecal vesicle, condition: (0) simple, (1) very large. Uninformative. A very large spermathecal vesicle is an autapomorphy for the genus *Modernacris*.

6.4 Discussion

6.4.1 Towards a phylogeny-based natural classification for Pyrgomorphidae

10 out of 21 tribes tested for monophyly were found to be monophyletic (Psednurini, Chlorizeini, Gymnohippini, Verdulini, Desmopterini, Monistriini, Dictyophorini, Atractomorphini, Tagastini, Chrotogonini) and can be recognized as natural groups. For the other eleven tribes that were not recovered as monophyletic, I propose to discontinue the use of their names. Based on the consensus tree of 446 trees, I have recognized the following clades.

Clade 1. Psednurini.

Synapomorphies: Fore and middle legs reduced (50:1), ventral lobe of hind knee reduced (62:1), long subgenital plate (90:1), galeae of the maxillae turn forward over the labrum

(118:1), absence of caecum of spermatheca (136:0). Diversity: 3 genera. *Psedna, Psednura, Propsednura*. Distribution: Australia.

Clade 2. Desmopterini.

Synapomorphies: Body compressed laterally (119:1) and tegmina sided parallel (120:1). Diversity: 10 genera (*Apodesmoptera Desmoptera, Desmopterella, Menesesia, Menesesiella, Stenoxyphus, Doriaella, Paradoriaella, Stenoxyphellus, Stenoxyphula*). Distribution: Northern Australia and South Pacific region to Philippines.

Clade 3. Chrotogonini.

Synapomorphies: A quadrate area between eyes in dorsal view (9:1) and the presence of a collar of prosternum (40:1). Diversity: 5 genera: *Chrotogonus*, *Stibarosterna*, *Tenuitarsus*, *Caconda, Shoacris*. Distribution: Africa and Asia.

Clade 4. Chlorizeini.

Synapomorphies: Eyes circular (22:0), area between mesosternal and metasternal space transversally rectangular (46:2), hind femur in males as long as abdomen (52:1), bridge of epiphallus constricted (90:1). Diversity: 8 genera: *Chlorizeina, Pterorthacris, Cawendia, Humpatella, Feacris, Pseudorubellia, Katangacris, Marsabitracris*. Distribution: Southeast continental Asia, Madagascar and tropical Africa.

Clade 5. *Acropyrgus, Gymnohippus* and *Pyrgohippus*.

Synapomorphies: Head as long as wide (5:1), texture of frons tuberculate (13:1), dorsal portion of the head tuberculate (15:1), absence of median carina of pronotum (38:0), lower marginal area of hind femur wider that upper marginal area (58:0). Diversity: 3 genera, *Acropyrgus, Gymnohippu*s and *Pyrgohippus*. Distribution: Madagascar.

Clade 6. *Schulthessia, Minorissa, Jaragua, Omura, Algete*.

Synapomorphies: Head longer than pronotum (6:2), transversally rectangular area between mesosternal and metasternal space (46:2). Diversity: 5 genera. Distribution: Madagascar and northern half of South America and Caribbean. Nested in this clade is a clade composed of genera *Omura, Algete, Minorissa* and *Jaragua* that possesses an uncontroverted synapomorphy namely the eye invading the fastigium in its posterior lateral border (121:1). Distribution. Northern half of South America and Caribbean. Kevan et al. 1974 proposed *Omura, Algete* and *Minorissa* to probably be related to *Schulthessia* due to external morphology.

Clade 7. Tagastini.

Synapomorphies: Antennae longer than head and pronotum (1:2), eyes circular (22:0), Presence of apical pocket if spematheca (127:1), short and prominent terminal dilation of spermathecal duct. Diversity: 2 genera, *Tagasta* and *Annandalea*. Distribution: Southeast Asia.

Clade 8. Atractomorphini.

Synapomorphies: A fuse bridge, lateral plates and lophi of the epiphallus (101:1) and a large and prominent terminal dilation of spermathecal duct (133:3) both uncontroverted. Diversity: 2 genera, *Atractomorpha* and *Occidentosphena*. Distribution: Sub-Saharan Africa, Asia, Australia and Pacific Islands.

Clade 9.

Synapomorphies: Metasternal lobes separated (42:1), columellae present (132:1). Diversity: 7 genera: *Calamacris, Ichthiacris, Sphenacris, Ichthyotettix, Piscacris, Pyrgotettix, Sphenotettix.* Distribution: Mexico. This New World Pyrgomorphidae clade is covered in detail in Chapter 5.

Clade 10.

Synapomorphies: Absence of carinula of fastigium of vertex (27:0), longer upper basal lobe of hind femur relative to lower basal lobe (54:2), vestigial process of cingulum (111:0), smooth posterior edge of subgenital plate (131:0). Diversity: 2 genera, *Meubelia* and *Spinacris.* Distribution: Philippines, Indonesia, Papua New Guinea, Solomon Islands. This clade is formed by a clade composed of *Meubelia* and *Spinacris* (that possesses three uncontroverted synapomorphies namely large valves of cingulum (123:1), large valves of aedagus (124:1) and sclerotized ornamentation of postvaginal sclerite (130:1). Additionally these two genera have a deep basal emargination of cingulum (122:2) and a dilated terminal of spermathecal duct (133:1). This clade is sister to a clade composed of *Tarbaleopsis*, *Modernacris* and *Tarbaleopsis*, and Kevan et al. (1971) mentioned a possible relationship between these two clades.

Clade 11.

This clade consisted of three main clades.

The first one consists of *Mekongiella* (China), *Rubellia* (Madagascar) and *Sphenarium* + *Prosphena* (Mexico to Costa Rica).

The second clade is composed of 7 genera: *Zonocerus, Physemophorus, Poekilocerus, Phymateus, Phyteumas, Paraphymateus, Rutidoderes*. All of them have in common a mid-dorsal abdominal gland. Distribution: Africa, Madagascar, Socotra Island, Asia.

The third clade is composed of 11 genera: *Petasida, Scutillya, Greyacris, Monistria Yeelanna, Parastria* (Australia), Aularches (Asia) and *Taphronota, Dictyophorus, Camoensia Maura, Loveridgacris, Parapetasia* (Africa). All Pyrgomorphidae that produce foam as a strategy for defense are placed here.

6.4.3 Evolution of wings and chemical defense

Wing reduction is common across Orthoptera, and the family Pyrgomorphidae is one of the families that show different types of wing reduction. As explained in Chapter 4, the absence of wings (apterous) is a straightforward characteristic in terms of description and so is the presence of fully developed wings (macropterous). In Pyrgomorphidae, I recognize two types of wing reduction and use the following descriptive terms. The first is micropterous, in which tegmina (first pair of wings) are present but atrophied and are no longer able to open (non-functional) and the second pair of wings is absent. The second term is brachypterous, in which tegmina and wings are reduced but still functional. I mapped onto my preferred most parsimonious tree the four conditions: apterous, micropterous, brachypterous, and macropterous using the DELTRAN optimization (fig. 6.17). The ancestral condition was macropterous with multiple and independent wing reductions across the phylogeny. However, some patterns emerge, for instance, the great majority of apterous Pyrgomorphidae occur in clade 2. In this clade the loss of wings is rampant with most species showing complete loss of wings and some cases of micropterism. Very few species show brachypterism and macropterism. On the other hand, in clade 3, there is a pattern of wing reduction but it is less severe than the clade 2, and in multiple subclades the macropterous condition persists. Also, there are more cases of partial wing reduction (brachypterism/still functional) although there are cases of dramatic wing reduction (micropterism). For the case

of intrapspecific wing polymorphism even in the same population, it is present across the phylogeny in the genera, *Psedna, Rubellia, Yeelanna, Monistria, Zonocerus, Maura, Parapetasia* and *Chrotogonus*. This wing polymorphism is variable and it could be macropterous/brachypterous form such as in *Rubellia, Monistria, Zonocerus,* and *Maura*. It could also be brachypterous/micropterous form such as in *Parapetasia*, macropterous/micropterous form such as in *Psedna,* and macropterous/brachypterous/ micropterous form as in *Chrotogonus*.

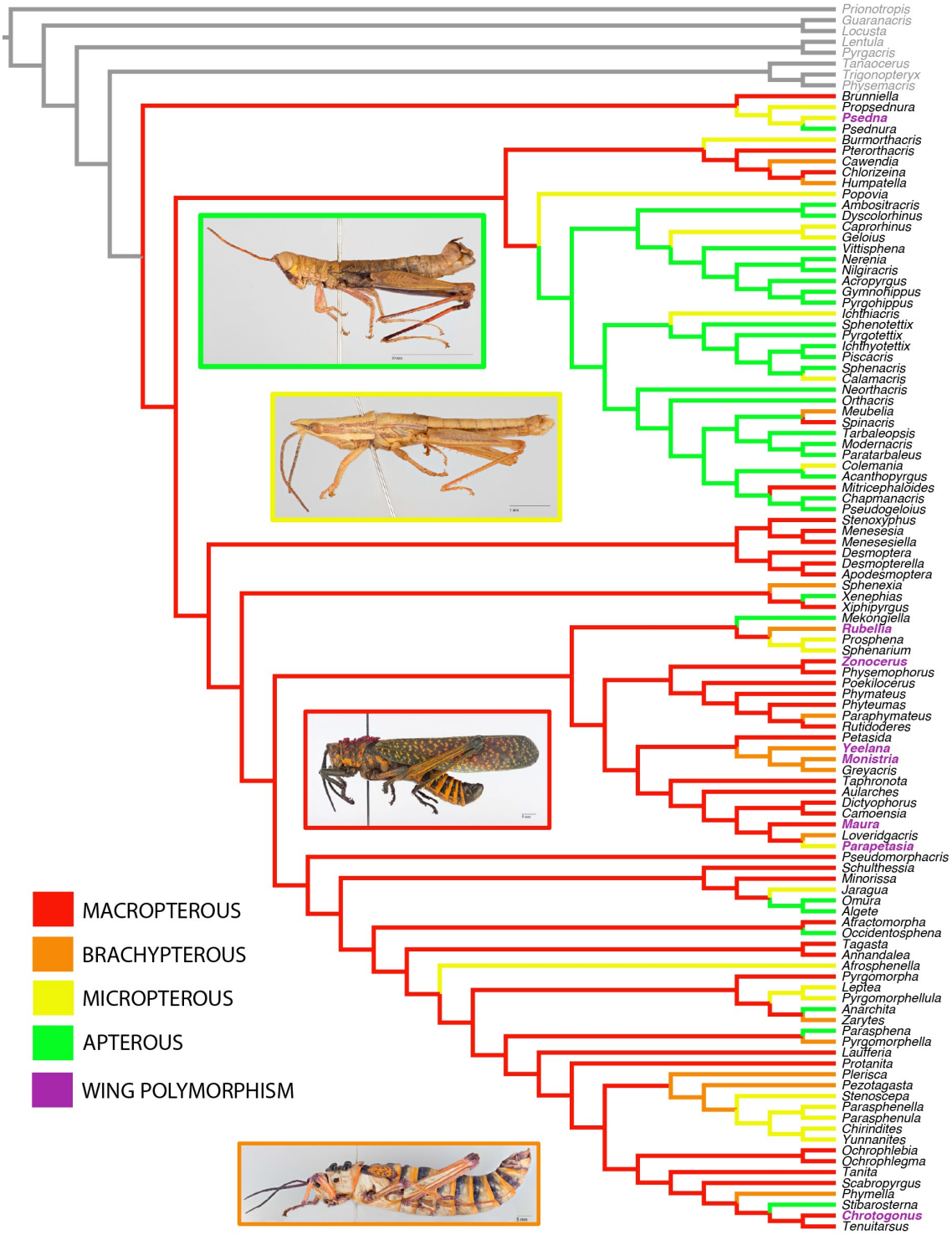

Figure 6.17. Character mapping of wing development in the preferred most parsimonious tree.

Chemical defense is present in Pyrgomorphidae and well documented in certain genera, such as *Zonocerus*, *Poekilocerus* and *Phymateus* (REF). Besides the body coloration, there are morphological structures involved in chemical defense, such as mid-dorsal abdominal glands and foam production as reviewed in Chapter 1. Based on my preferred most parsimonious tree, it is possible to hypothesize that the evolution of aposematic coloration occurred at least four independent times (fig. 6.18). However, there is one particular clade that contains most of the genera with aposematic coloration. In this clade, it is possible to distinguish three patterns shown in the three different clades. In the clade consisting of *Zonocerus, Physemophorus, Poekilocerus, Phymateus, Phyteumas, Paraphymateus,* and *Rutidoderes,* there is a presence of a mid-dorsal abdominal gland that ejects distasteful content as a warning signal when disturbed (REF). There is only one other genus reported to possess such a gland (*Colemania*), which is outside this clade. In the clade consisting of *Petasida, Scutillya, Greyacris, Monistria Yeelanna,* and *Parastria,* there are no specialized morphological structures involved in chemical defense. Finally, in the clade consisting of *Aularches*, *Taphronota, Dictyophorus, Camoensia, Maura, Loveridgacris,* and *Parapetasia,* there is an unique element of chemical defense, namely foam production, which has been well documented (REF). Judging from the observed patterns, it is reasonable to assume that aposematic coloration is a phylogenetically conserved trait, although the specific mechanisms may vary within this clade. There is one caveat though. I have used the term aposematic quite loosely to refer to typical warning coloration (e.g. contrasting between black and yellow/red), but the presence of true aposematic coloration needs to be empirically tested for unprofitability in taste, smell or both and this has not been done for all the genera involved.

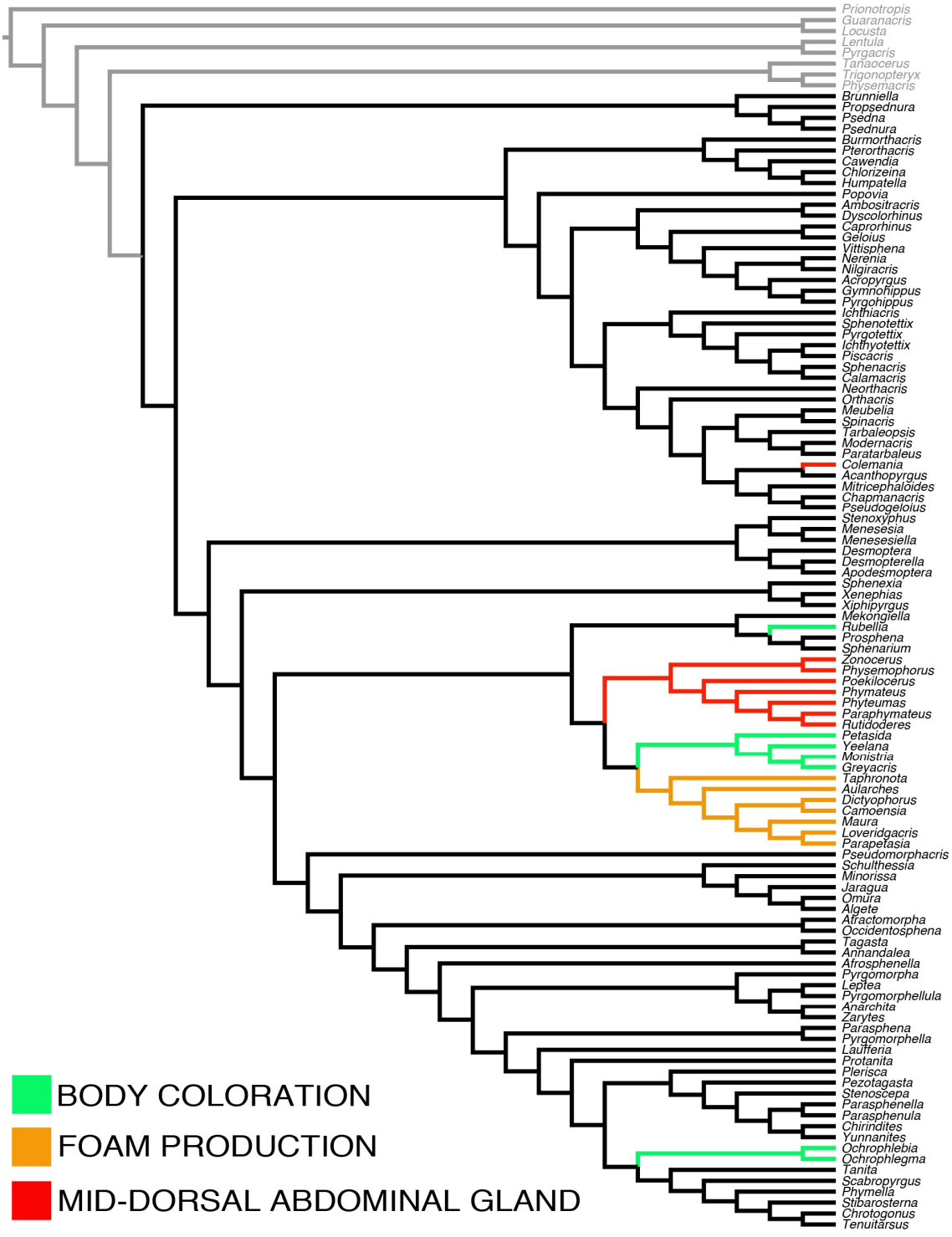

Figure 6.18. Different expressions of chemical defense in the preferred most parsimonious tree.

6.5 Conclusions and future directions

This study is the most comprehensive attempt to date in resolving the phylogeny of Pyrgomorphidae in terms of both taxon and morphological character sampling. Despite the fact several nodes collapsed when applying the consensus to the 446 equally parsimonious trees, some patterns emerge and allow us to test Kevan's concepts of tribes. The test of monophyly of these tribes is the first step towards a phylogeny-based natural classification. It is imperative not to fall in the same pattern of oversplitting, and although is valid to name monotypic clades, this needs to be reserved only when a strong argumentation can be made. For instance, the first of the three clades that I proposed consists of only four genera compared to 34 and 66 of the second and third clades, respectively, but the synapomorphies for this first clade, such as galeae turn forward to cover the labrum and an elongate subgenital plate, are uniquely derived enough to justify naming this clade. I consider it better to recognize a few well-justified clades than to continue with Kevan's scheme of 31 tribes, which I show to be paraphyletic in many cases. Although I did not specifically elaborate, several of Kevan's tribes included many subtribes, I find that such fine division of groups that may or may not be monophyletic would actually defeat the purpose of classification. In this study, I find that geographical distribution is more indicative of evolutionary relationships rather than morphological characters (fig. 6.19), and considering the old age of this family, it is plausible that the present-day Pyrgomorphidae fauna is relictual and is heavily influenced by convergent evolution in external morphology, which has played a crucial role in misleading cladistic analyses. Nevertheless, the inclusion of female characters has vastly improved the phylogenetic resolution from my previous character coding, which focused heavily on male characters. Therefore, only the careful inspection of morphology, in light of

phylogenetic relationships informed by molecular data, which might be less affected by convergence, will allow me to disentangle difficult relationships in the future.

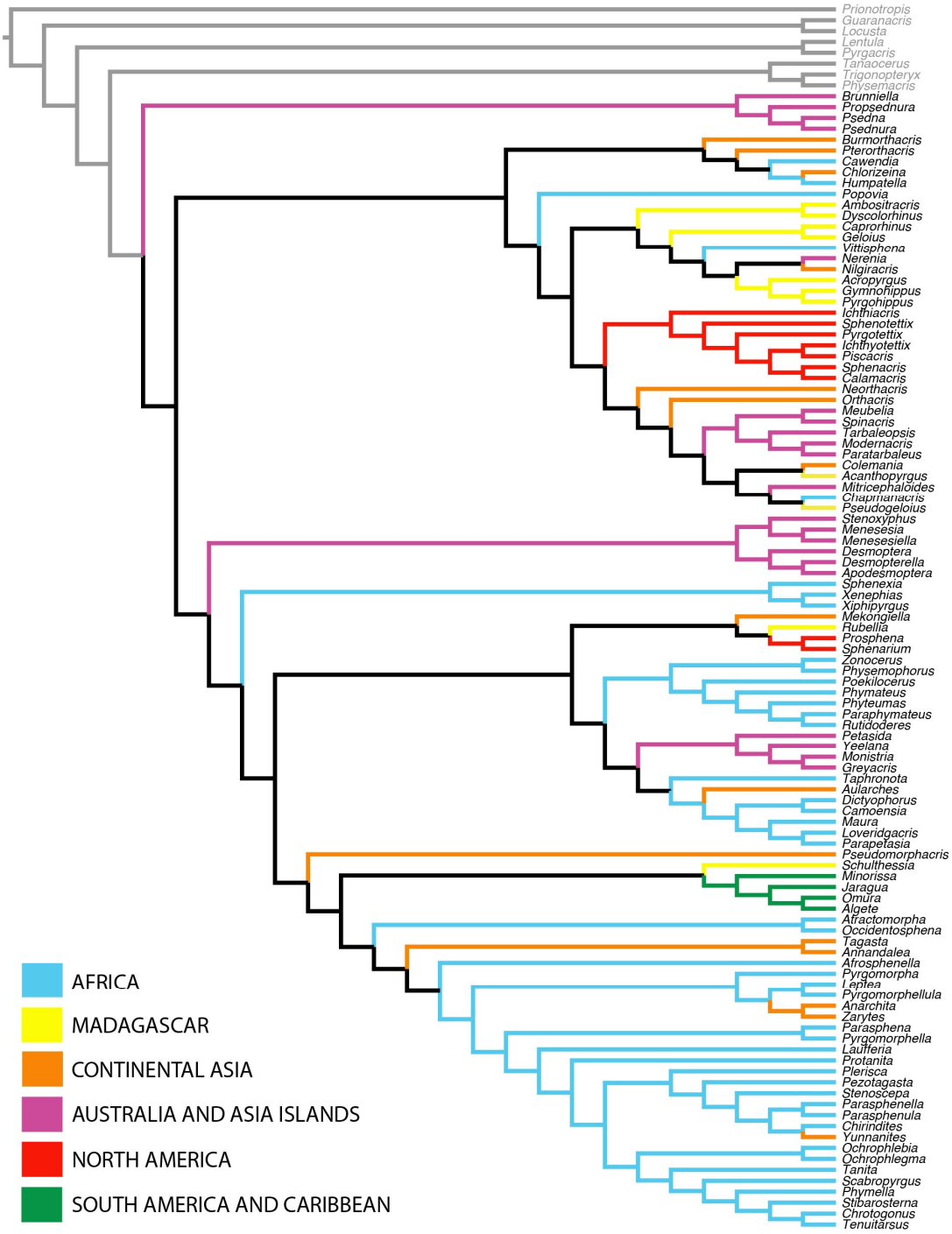

Figure 6.19. Geographical distribution in the preferred most parsimonious tree. North America is considered from USA to Panama.

CHAPTER VII

CONCLUSION

The taxonomy of the family Pyrgomorphidae had been abandoned for more than forty years before this dissertation, and although the literature about this family is abundant, there had never been a systematic study for the entire family in a phylogenetic framework. For this dissertation, I aimed to substantially improve the systematics of this family by developing taxonomic expertise in this group by taking the following steps, each of which resulted in its own chapter.

The first step was to get acquaintance with the group and several visits to the most important collection in North America and Europe harboring Pyrgomorphidae were made in order to obtained photographic records of type material and borrow non-type material for my study. As a result, I was able to make a major contribution to digitize Pyrgomorphidae type material, which was made available through the online catalogue Orthoptera Species File. Before my graduate work, only 15% of the type specimens of the valid species were available in color. Through numerous museum visits, I was able to increase this figure to 85%. At the same time, multiple type material of synonyms were also documented, and when available, I borrow non-type material to gather the most comprehensive Pyrgomorphidae collection in the world with 105 out of 149 genera representing approximately half of the current valid species (487). Additionally, with these museums visits, the catalogue of type depository was curated and updated.

The second step, once familiarized with the Pyrgomorphidae diversity, was to gather all the identification keys available for the groups, which I found to be collectively outdated, incomplete, and unfriendly because they were in different languages such as Chinese, French,

Portuguese and Spanish. Also, in most cases, they were poorly illustrated, so my task was to completely update, translate, and illustrate them. As a result, 12 regional profusely illustrated keys in English to the Pyrgomorphidae genera of the world were constructed to synthetize the entire genera diversity for the family in a single document.

The third step was to conduct a phylogenetic analysis using morphological evidence for the family based in a representative taxon sampling for a first time ever. As a result, the monophyly of the family and subfamilies was tested and the internal relationships started to be elucidated. The family Pyrgomorphidae was recovered as a monophyletic group and only one of the two subfamilies was monophyletic.

This led me to the fourth step that included the use of the entire mitochondrial genomes plus four nuclear genes in a subset of the family with a strong emphasis in the New World Pyrgomorphidae to study its origin. This molecular phylogenetic analysis again recovered Pyrgomorphidae as a monophyletic group and allowed me to infer some phylogenetic relationships that were neglected due to convergence in the morphological analysis. Through this step, I realized that geographic distribution could be highly informative and very frequently mirror evolutionary patterns. Furthermore, I was able to test different hypotheses about the origin of the New World Pyrgomorphidae in a statistical framework.

The last step of this learning process was to test the current classification system proposed by Kevan et al. (1969, 1970, 1971, 1972, 1974, 1975) with an expanded taxon sampling and addition of new morphological evidence. The results showed that the current classification, although informative and helpul, does not reflect phylogeny and the entire phylogeny needs to be reclassified. In this expanded morphological phylogeny, the Pyrgomorphidae was again recoverd as a monphyletic group but now both subfamilies were shown to be paraphyletic. I recognized

three main clades and discussed the importance of reflecting phylogeny in order to prevent overspliting into artificial groupings, and to maximize the utility of taxonomic classification.

It is hard to believe that this family, which is considered one of the most colorful grasshoppers in the world and contain some of the most spectacular examples of aposematic coloration, chemical defense, bizarre spines and tubercles on the pronotum, has never been studied in a phylogentic framework. It is interesting to have in the same document a record of the typical stages (5 steps that I described above) that occur in a systematic study of a given taxa. Sometimes these stages happen in the course of many years and are not registered in a single document. To provide an example of this, take an Australian group of Pyrgomorphidae, the psednurines, for example. In my first approach to elucidate the relationships of the family (Chapter 4) using only morphological evidence, this group was recovered as one of the most derived clades. Later on when using molecular evidence (Chapter 5), this group was recovered as the most basal clade within Pyrgomorphidae. This conundrum was challenging, but due to this reciprocal illumination, I was able to disentagle some morphological characters that were otherwise not taken into account, which provided evidence in an expanded morphological study (Chapter 6). As a result, there is now morphological evidence of the basal placement of this group in the phylogeny of Pyrgomorphidae. This evolution of knowledge clearly examplifies the purpose of a dissertation.

I was able to examine the evolution of very intersting features in this family, such as wing reduction and various modes of chemical defense and aposematism based on the findings in Chapters 4, 5, and 6. With the evidence gathered, it is possible to conclude that wing reduction was rampant throghout the family and that foam production, mid-dorsal abdominal gland and striking coloration evolved separately and have taken different evolutive pathways.

This study has provided the solid foundations for the systematics of Pyrgomorphidae and it is cornerstone for future investigation of this intriguing family of grasshoppers.

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APPENDIX A

PYRGOMORPHIDAE OF ECONOMIC IMPORTANCE (BASED ON COPR, 1982)

Species	**Country**	**Economic importance**	**Crops damaged**
Orthacris incongruens	India	G	Tea, tobacco
Orthacris robusta	India	G	Tea, dadap, coffee, citrus and *Grevillea* sp.
Orthacris ceylonica	Sri Lanka	K	Citrus, dadap and *Gliricidia* sp.
Orthacris filiformis	Sri Lanka	K	Citrus, mango
Orthacris spp.	India		Aubergine, bulrush millet, cabbage, finger millet, groundnut, maize, sorghum, tea, coffee, tobacco, dadap
Neorthacris simulans	India	E	*Rauwolfia serpentina*, aubergine, bulrush millet, cabbage, finger millet, foxtail millet, groundnut, lablab, safflower, sorghum, sunflower
Neorthacris acuticeps	India	G	Aubergine, indigo, mulberry, sandalwood, sweet potato
Neorthacris longicercata	India	H	Aubergine, bulrush millet, cabbage, finger millet, groundnut, sorghum
Neorthacris malabarensis	India	K	Tea, cinchona
Colemania sphenarioides	India	D	Bulrush millet, chilli, common millet, cotton, cowpea, finger millet, foxtail millet, groundnut, guinea corn, lablab, maize, millets, *Phaseolus* spp., pigeon pea, rice, sorghum, wheat
Desmopterella explicata	Papua New Guinea, Indonesia, Australia	K	Cacao, cassava, brussels sprouts, Chinese cabbage, potatoes
Desmopterella biroi	Papua New Guinea	K	Cacao, sweet potato, oil palms, rice
Chlorizeina feae	Thailand	E	Maize, *Eupatorium odoratum*, bamboo, castor, cucumber, rice, sorghum, soybean
Chlorizeina unicolor	India, Myanmar, Thailand, Laos	K	Teak
Chlorizeina togulata	Myanmar	K	Teak
Poekilocerus bufonius vittatus	Saudi Arabia, Yemen, Oman, Ethiopia, Djibouti, Somalia	G	Tomatoes, aubergines, tobacco
Poekilocerus pictus	Afghanistan, Pakistan, India	D	Aubergine, bamboo, banana, cabbage, canna, castor, chilli, citrus, Clerodendrum sp., cotton, cucurbits, grape vines, *Luffa acutangula*, mango, melon, okra, oleander, papaya, *Pinus longifolia*, potato, sorghum, sugar cane, tomato

Species	Country	Economic importance	Crops damaged
Zonocerus elegans	Kenya, Uganda, Tanzania, Mozambique, Democratic Republic of the Congo, Rwanda, Malawi, Zambia, Angola, Zimbabwe, Madagascar, Namibia, Botswana, South Africa, Lesotho	C	Apple, apricot, banana, cabbage, camphor, cassava, castor, citrus, cocoa, coffee, cotton, cowpea, fig, grapes, groundnut, lettuce, lucerne, maize, melon, mulberry, onion, papaw, peach, pear, pigeon pea, pineapple, plum, potato, pumpkin, quince, rubber, sorghum, spineless cactus, sugar cane, sunflower, sweet potato, tobacco, tomato
Zonocerus variegatus	Africa south of the Sahara, includin Ethiopia ans as fas as Angola, Democratic Republic of the Congo and Kenya	C	Annatto, apricot, avocado, banana, breadfruit, bulrush millet, cabbage, carrot, cashew, cassava, castor, citrus, cocoa, coconut, cocoyam, coffee, cotton, cucumber, cowpea, date palm, fig, finger millet, kidney bean, kola, lime, maize, mango, mint, oil palm, okra, onion, papaya, peach, *Pennisetum*, peppers, pineapple, potato, pumpkin, rie, rubber, sesame, sorghum, soybean, sugar cane, sunflower, sweet potato, teak, tobacco, tomato, water melon, yam
Rutidoderes squarrosus	Gambia, Sierra Leone, Guinea, Ivory Coast, Ghana, Togo, Nigeria, Cameroon, Equatorial Guinea, Gabon, Democratic Republic of the Congo, Tanzania	K	Orange, grapefruit, *Tephrosia candida*
Phyteumas purpurascens	Ethiopia, Kenya, Tanzania, Democratic Republic of the Congo, Uganda, Malawi	H	*Hibiscus* and *Thevetia*
Phymateus leprosus	Swaziland, South Africa, Lesotho, Namibia, Zimbabwe	E	Beans, lettuce, peas, peach, citrus, pumpkin, sunflower, oleander

Species	Country	Economic importance	Crops damaged
Phymateus baccatus	South Africa, Namibia, Botswana, Angola, Zimbabwe	G	Crops
Phymateus aegrotus	Sudan, Ethiopia, Kenya, Somalia, Tanzania, Uganda	E	Cowpeas, cabbage, brassicas, lettuce, maize, potato, sorghum, spinach, sweet potato, tomato, various cereals, cucurbits, water melon
Phymateus pulcherrimus	Ethiopia, Somalia	H	Carrot, castor, lettuce, radish, *Tropaeolum*, finger millet
Phymateus morbillosus	South Africa, Zimbabwe	G	Crops
Phymateus saxosus	Madagascar	G	Coffee, rice, tobacco
Phymateus madagassus	Madagascar	G	Coffee, rice, tobacco
Phymateus viridipes	Sudan, Ethiopia, Kenya, Somalia, Tanzania, Uganda, Democratic Republic of the Congo, Angola, Zambia, Malawi, Mozambique, South Africa, Botswana, Rwanda	C	Vine, fig, all citrus species, cabbage, cassava, cassia, castor, coffee, cotton, *Eucalyptus*, *Euphorbia tirucalli*, fennel, finger millet, Gmelina, gourd, lavender, lettuce, loquat, lucerne, maize, mango, onion, papaya, pea, peach, pear, pepper, pomegranate, rice, sage, strawberry, sunflower, tobacco, tomato, beans, cashew, groundnuts, soya
Phymateus karschi	Mozambique, Tanzania	C	
Phymateus cinctus	Senegal to southwest Kenya	C	Peas, cotton, potato, *Thevetia*
Aularches miliaris	Pakistan, India, Nepal, Bangladesh, Sri Lanka, Myanmar, Thailand, Cambodia, Vietnam, Malaysia, Indonesia	D	Annatto, banana, beans, betel nut, breadfruit, cacao, cardamom, cashew, cassava, castor, chilli, cinchona, coconut, coffee, cotton, custard apple, dadap, date palm, durian, finger millet, guinea corn, guava, jackfruit, jute, longan, maize, mango, oil palm, pigeon pea, Pinus merkusii, plantain, rice, rubber, *Shorea robusta*, sesame, sugar cane, tea, teak, tobbacco, citrus
Species	**Country**	**Economic**	**Crops damaged**

		importance	
Taphronota calliparea dimidiate	Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Nigeria, Cameroon, Central African Republic, Sudan, Ethiopia, Equatorial Guinea, Gabon, Congo, Democratic Republic of the Congo, Burundi, Rwanda, Kenya, Uganda, Tanzania, Angola	E	Canna, cotton, granadilla, maize, pasture grasses, citrus, finger millet, sweet potato, *Mucuna stans*, *Bougainvillaea* sp., *Tecoma stans*, *Calodendron capense*, *Cupressus lindleyi*, *C. lusitanica*
Taphronota calliparea calliparea	Somalia, Kenya, Democratic Republic of the Congo, Tanzania, Angola, Zambia, Malawi, Mozambique, Zimbabwe, Botswana, Namibia, Lesotho, Swaziland, South Africa	E	As above
Taphronota ferruginea	Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Benin, Nigeria, Cameroon, Equatorial Guinea, Gabon, Central African Republic, Congo, D.R of the Congo, Uganda, Kenya, Tanzania	G	Citrus, coffee, cotton
Species	**Country**	**Economic**	**Crops damaged**

		importance	
Maura lurida	Sierra Leone, Ghana, Togo, Benin, Nigeria, Cameroon, Kenya, Uganda, Sudan, Ethiopia, Tanzania, Democratic Republic of the Congo, Rwanda, Malawi, South Africa, Angola, Mozambique	K	Farm crops
Maura bolivari	Democratic Repubic of the Congo, Tanzania, Malawi	K	Tobacco, coffee
Dictyophorus griseus	Guinea, Sierra Leone, Ivory Coast, Ghana, Togo, Nigeria, Cameroon, Sudan, Ethiopia, Somalia, Democratic Republic of the Congo, Uganda, Kenya, Rwanda, Burundi, Tanzania, Mozambique, Angola, Zambia, Zimbabwe, Malawi, Namibia	H	Coffee, cotton, roses, tobacco
Tagasta marginella	Thailand, Cambodia, Malaysia, Indonesia	K	Coconut, rice, sweet potato
Atractomorpha acutipennis	Sub-Saharan Africa, southwest Arabia Peninsula, Iran, Afganistan, Pakistan	G	Cotton, legumes, lucerne, rice, spinach, sweet potato, tobacco, Torenia, aubergine
Species	**Country**	**Economic importance**	**Crops damaged**

Atractomorpha angusta	Nepal, Bhutan, India, Bangladesh, Myanmar, Thailand, Cambodia, Laos, Vietnam, west Malaysia, Singapore, Indonesia	G	Aubergine, cotton, maize, rice, soya, tea, tobacco
Atractomorpha crenaticeps	Borneo, Philippines, Talaud, Moluccas, Admiralty, New Guinea, Bismarck, Solomon, Hawaiian Islands	H	Aubergine, cacao, coffee, coconut, cruciferous crops, rosella, sugar cane, sweet potato, tobacco
Atractomorpha crenulata	Maldives, Sri Lanka, India, Nepal, Bangladesh, Myanmar, Thailand, Cambodia, Laos, Vietnam	C	Tobacco, maize, *Acrocarpus fraxinifolius*, arrowroot, *Artocarpus hirsuta*, aubergine, barley, cabbage, castor, cauliflower, chillies, citrus, cotton, fenugreek, finger millet, gram, groundnut, jute, lucerne, mints, oats, pea, peach, radish, rice, sorghum, sugar cane, sunn hemp, sweet potato, wheat, *Zinnia*, opium
Atractomorpha burri	As above	C	As above
Atractomorpha lata	China, Korea, Japan	E	Aubergine, barley, beans, buckwheat, camphor tree, carrot, cherry, chrysanthemum, citrus, cotton, dahlia, foxtail, millet, hemp, maize, millet, mulberry, orange, radish, rice, *Rubus* spp., sesame, sugar bet, sugar cane, soybean, tomato, wheat
Atractomorpha psittacina	India, Bangladesh, Myanmar, China, Philippines, Cambodia, Thailand, Laos, Vietnam, Malaysia, Singapore, Indonesia.	G	Asparagus pea, aubergine, cabbage, cacao, coconut, cotton, groundnut, jute, kapok, kidney bean, lablab, legumes, lettuce, lima bean, maize, mulberry, mung bean, mustard, peas, pigeon pea, pse-tsai, radish, rice, sorghum, soybean, sugar cane, sweet potato, tobacco
Species	**Country**	**Economic importance**	**Crops damaged**
Atractomorpha	Indonesia, Malaysia		Sugar cane

rhodoptera			
Atractomorpha similis	New Guinea Island, north and east Australia	K	Cruciferous crops, groundnuts, lettuce, sugar cane, rubber, sweet potato, cabbage, cotton
Atractomorpha sinensis	India, China, Vietnam Taiwan, Line, Mariana, Marshall, Hawaiian Islands	G	Apple, aubergine, barley, beans, camphor, carrots, Chinese cabbage, citrus, cotton, ginger, *Ipomoea aquatica*, millet, mulberry, mustard, New Zealand spinach, onion, parsley, pineapple, potato, rice, *Scaevola chamissoniana*, soybean, sugar beet, sugar cane, sweet potato, tomato
Rubellia nigrosignata	Madagascar	H	Rice
Sphenarium purpurascens	Mexico	D	Maize, barley, chilli, kidney beans, lucerne, orange, sorghum, soybean, sweet potato, tobacco, vine
Pyrgomorpha vignaudi	Mauritania, Senegal, Gambia, Guinea Bissau, Guinea, Sierra Leone, Mali, Niger, Sudan, Ethiopia, Ghana, Nigeria, Cameroon, Equatorial Guinea, Congo, Democratic Republic of the Congo, Uganda, Rwanda, Kenya, Tanzania, Malawi, Angola	G	Groundnut, cotton, potato, sorghum, tobacco turnips, cabbage, castor, maize, pumpkin, soya, tomato
Pyrgomorpha bispinosa	North, west and east Africa, except Somalia and north Kenya, Arabic Peninsula, southwest and central Asia eastwards to India, Sinkiang and Mongolia	E	Castor, cotton, cucumber, groundnut, lablab, lavender, lucerne, melon, pepper, potato, safflower, sesame, sorghum, squash,wheat
Species	**Country**	**Economic importance**	**Crops damaged**
Pyrgomorpha conica	Upper half of Africa, Arabic Peninsula,	E	As above

	Mediterranean and Iberian regions		
Pyrgomorpha cognate	From Mauritania, Senegal and Mali to Israel, Arabic Peninsula and Pakistan	E	As above
Pyrgomorpha guentheri	Syria, Israel and Turkey to Iran, the Caucasus and Turkmenistan		
Pyrgomorphella arachidis	Kenya, Tanzania, Malawi	E	Groundnut
Chrotogonus hemipterus	Angola, Democratic Republic of the Congo, Rwanda, Burundi, Tanzania, Kenya, Namibia, Zambia, Malawi, Zimbabwe, Mozambique, Botswana, Swaziland, South Africa	F	Cabbage, castor, coffee, cotton, groundnuts, *Hibiscus* sp., kidney bean, legumes, maize, melon, millet, *Pinus patula*, radish, tobacco, tomato, pigeon pea, sesame, soybeans
Chrotogonus homalodemus	Niger, Chad, Egypt, Sudan, Ethiopia, Kenya, Tanzania, Djibouti, Somalia, Yemen, Saudi Arabia, Israel, Oman, Iran, Pakistan	F	Beans, beets, bulrsuh millet, cereals, clover, cotton, date, guinea corn, maize, oil seeds, rice, tobacco, tomato, wheat
Species	**Country**	**Economic importance**	**Crops damaged**
Chrotogonus oxypterus	Sri Lanka, India, Bangladesh	F	Blue gum, lemon scented gum, bulrush millet, coffee, cotton, finger millet, guinea corn, maize, rice, tobacco, wheat
Chrotogonus senegalensis	Mauritania, Senegal, Gambia, Guinea Bissau, Guinea, Sierra	G	Cereals, coffee, cowpeas, finger millet, guinea corn, maize, millets, oil palm, potatoes, tobacco, *Zinnia*, bulrush millet, citrus, groundnuts, radish

	Leone, Liberia, Ivory Coast, Ghana, Togo, Benin, Mali, Niger, Nigeria, Chad, Sudan, Central African Republic, Ethiopia, Cameroon, Congo, Democratic Republic of the Congo, Burundi, Uganda, Rwanda, Kenya, Angola, Zambia		
Chrotogonus trachypterus	Afghanistan, Iran, Pakistan, Nepal, Bangladesh, India	D	Aubergine, barley, *Boerhavia repens*, bulrush millet, cabbage, calabash, carrot, castor bean, catjang, cauliflower, chick pea, cluster bean, cotton, cowpea, cucurbits, flax, groundnut, guinea corn, indigo, jute, lucerne, maize, melon, millet, mustard, oats, okra, opium poppy, pea, *Phaseolus* sp., *Pinus longifolia*, potato, rape seed, rice, Robinia sp., safflower, sesame, sugar cane, tobacco, tomato, vetch, wheat

APPENDIX B

LABEL INFORMATION OF THE SPECIMENS USED IN CHAPTER IV

Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
Chapmanacris sylvatica	male	Ghana	Western Region	2. 1. 1959	R.F. Chapman	David Hollis, 1965	BMNH
	female	Ghana	Eastern Region	13. 11. 1962	N.D.Jago	David Hollis, 1965	BMNH
Pseudogeloius decorsei	male	Madagascar	CAP Sainte MARIE	9. 5. 1968	Mission White	M. Descamps. 1966, D. Wintrebert 1969	MNHN
	female	Madagascar	LAVONONO	15. 3. 1968	G. Cadet	M. Descamps. 1966, D. Wintrebert 1969	MNHN
Gymnohippus marmoratus	male	Madagascar	Beheloka	3. 5. 1963	D. Wintrebert	Bruner 1910, M. Descamps 1963	MNHN
	female	Madagascar	LAVONONO (Betindria)	27. 2. 1964	D. Wintrebert	Bruner 1910, M. Descamps 1966	MNHN
Sphenacris crassicornis	male	Mexico	5 mi E Ciudad Maiz, S.L. P. 4500ft	1. 9. 1940	H.R. Roberts	Asket Singh, 1964	ANSP
	male	Mexico	6 mi W. Ciudad Maiz, S. L. P. 4500ft	9. 9. 1940	H. R. Roberts	Asket Singh, 1964	ANSP
	female	Mexico	5 mi W. Naranjos On R. Saltos, S. L. P. 500ft	30. 8. 1940	H. R. Roberts	Asket Singh, 1964	ANSP
	female	Mexico	3-8 mi N. Jacala 5-600ft	1. 9. 1936	H. R. Roberts	Asket Singh, 1964	ANSP
Mitricephaloides rhodopterus	male	Malaysia	Klano Gates	17. 7. 1933	N. C. E. Miller	Miller 1922, B. Uvarov 1933, D. K. McE. Kevan 1962	BMNH
	female	Malaysia	Kuala Sleh. K Lumpur	8. 9. 1940	N. C. E. Miller	D. K. McE. Kevan 1957	BMNH
Modernacris controversa	male	Solomon Island	Munda (New Georgia)	15. 8. 1963	M. McQuillan	V. M. Dirsh 1964	BMNH
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**

Acroprygus cadeti	male	Madagascar	Beheloka	12. 4. 1963	D. Wintrebert	Descamps 1963, M. Descamps DET 1966	
	female	Madagascar	Beheloka	12. 4. 1963	D. Wintrebert	Descamps 1963, M. Descamps DET 1966	
Caprorhinus kevani	male	Madagascar	Satrikala (Horombe)	22. 1. 1968	D. Wintrebert	Descamps & Wintrebert 1966, D. Wintrebert 1969	
	female	Madagascar	15 KM. SW. Ranohira (Isalo)	26. 1. 1968	D. Wintrebert	Descamps & Wintrebert 1966, D. Wintrebert 1969	
Orthacris incongruens	male	India	Nilgiri Hills (Madras Pres.)	Fall 1921	A.P. Nathan	Hebard 1924, Asket Singh 1964	ANSP
	male	India	Nilgiri Hills (Madras Pres.)	Fall 1921	A.P. Nathan	Hebard 1924, Asket Singh 1964	ANSP
	female	India	Nilgiri Hills (Madras Pres.)	Fall 1921	A.P. Nathan	Hebard 1924, Asket Singh 1964	ANSP
	female	India	Nilgiri Hills (Madras Pres.)	Fall 1921	A.P. Nathan	Hebard 1924, Asket Singh 1964	ANSP
Colemania sphenarioides	male	India	Kodumur (Kurnool DT.)	23. 9. 1916	T.V.R. CoU		BMNH
	female	India	On sorghum crop (LOT BA 25) from the agri. Comp. ICRISAT.	30. 10. 75	K.V. S.	N.D. Jago 1977	BMNH
Acanthopyrgus finoti	male	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m.	12. 1936 to 4.1987	C. Lamberton	D. K. McE. Kevan 1963	ANSP
	male	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m	12. 1936 to 4.1987	C. Lamberton	D. K. McE. Kevan 1963	ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
	female	Madagascar			C.	Herbard 1924, D. K.	ANSP

					Lamberton	McE. Kevan 1963	
	female	Madagascar			De Saussure	Herbard 1924, D. K. McE. Kevan 1963	ANSP
Meubelia leytensis	male	Philippines	Dagamy (Leyte), Mt. Lobi	21. 6. 1945	E.R. Helwig	D. K. McE. Kevan 1973	ANSP
	male	Philippines	Dagamy (Leyte), Mt. Lobi	21. 4. 1945	E.R. Helwig	D. K. McE. Kevan 1973	ANSP
	female	Philippines	Dagamy (Leyte), Mt. Lobi	27. 9. 1945	E.R. Helwig	D. K. McE. Kevan 1973	ANSP
	female	Philippines	Dagamy (Leyte), Mt. Lobi	19. 7. 1945	E.R. Helwig	D. K. McE. Kevan 1973	ANSP
Atractomorpha aberrans	male	Congo	Sanga R. (Nola), Elev. 1800 ft.	31. 10. 1934	J. A. G. Rehn		ANSP
	female	Cameroon	Ebolowa	13. 4. 1932	H. C. Wing		ANSP
	female	Cameroon	Ebolowa	12. 1. 1932	H. C. Wing		ANSP
Chlorizeina unicolor	male	Thailand	5 km E. Sar??L. AH LOT JR 641220	27.10. 1964	J. Roffey, Smut		BMNH
	female	Thailand	5 km W. Rong Kwang LOT 64958	8. 10. 1964	J. Roffey, Smut		BMNH
Humpatella huambae	male	Angola	5 mi NE Negola	25. 3. 1972			BMNH
	female	Angola	5 mi NE Negola	25. 3. 1972			BMNH
Chrotogonus oxypterus	male	India	Coimbatore (Madras Pres)	7. 1. 1921	A. P. Nathan	Hebart 1924, D. K. McE. Kevan 1953	ANSP
	female	India	Chepat Polur	17. 4. 1931	P. S. Nathan	D. K. McE Kevan 1953	ANSP
	female	India	Trichinopoly (Madras Pres.)	1. 8. 1921	C. Leigh	D. K. McE Kevan 1953	ANSP
	male	India	Chepat Polur	17. 4. 1931	P. S. Nathan	D. K. McE Kevan 1953	ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
Tenuitarsus	male	Mauritania	Coppolani	25. 8. 1936	CH.	Blanchard 1836, M.	MNHN

angustus					Rungs	Descamps 1986	
	female	Mauritania	Coppolani	25. 8. 1936	CH. Rungs	Blanchard 1836, M. Descamps 1986	MNHN
Desmopterella angustata	male	Indonesia	Maffin Bay (Dutch)	10. 9. 1944	E. S. Ross Coll.	D. K. McE Kevan 1968	ANSP
	male	Indonesia	Maffin Bay (Dutch)	4. 9. 1944	E. S. Ross Coll.	D. K. McE Kevan 1968	ANSP
	female	Indonesia	Maffin Bay (Dutch)	10. 6. 1944	E. S. Ross Coll.	D. K. McE Kevan 1959	ANSP
	female	Indonesia	Maffin Bay (Dutch)	19. 6. 1944	E. S. Ross Coll.	D. K. McE Kevan 1959	ANSP
Dictyophorus spumans	male	South Africa	Pakhuis Pass, Clanwilliams (Cape Province)	3. 1. 1940	R. H. N. Smothers		ANSP
	male	South Africa	Pakhuis Pass, Clanwilliams (Cape Province)	3. 1. 1940	R. H. N. Smothers		ANSP
	female	South Africa	betw. Fraserburg & Fraserburg (Cape Province)	20. 3. 1939	E.R. Helwig		ANSP
	female	South Africa	betw. Fraserburg & Fraserburg (Cape Province)	20. 3. 1939	E.R. Helwig		ANSP
Ichthyotettix mexicanus	male	Mexico	226 km NW Tehuacan, Pbla. 6500 ft	25. 8. 1936	H. R. Roberts	Asket Singh 1964	ANSP
	male	Mexico	Rd. N. Tehuacan, Pbla. to Orizaba 5500ft	1. 9. 1936	H. R. Roberts	Asket Singh 1964	ANSP
	female	Mexico	Tula River. Tasquillo. Hidalgo 5500ft	9. 9. 1936	H. R. Roberts	Asket Singh 1964	ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
	female	Mexico	196 km bet.	8. 8. 1936	H. R.	Asket Singh 1964	ANSP

			Zimapan & Ixmiquipan, Hidalgo 6000ft		Roberts		
Monistria concinna	male	Australia	Bull's head (A. C. T.) 4325-4350ft	18. 2. 1944.	K. H. L. & B. Key	J. A. G. Rehn 1949	ANSP
	male	Australia	Hotel Kosclusko (N. S. Wales) 5300 ft	18. 4. 1937	K. H. L. & B. Key	J. A. G. Rehn 1949	ANSP
	male	Australia	Mt. Buller (Victoria) 1650- 1800m	7. 2. 1982	K. H. L. & B. Key	K. H. L. & B. Key	ANSP
	female	Australia	Mt. Kosciusko (N.S.Wales) 5000 ft	15. 12. 1931		J.A. G. Rehn 1949	ANSP
	female	Australia	Mt. Kosciusko (N.S.Wales) 5000 ft	11. 12. 1931	L.F. Graham	J.A. G. Rehn 1949	ANSP
	female	Australia	Mt. Buffalo (Victoria)	21. 2. 1947.	Key, Carne & Rothery	J. A. G. Rehn 1949, K. H. L. & Key 1984	ANSP
Omura congrua	male	Ecuador	Hacienda La Mascota, Rio Topo, Alt. 4500ft	27. 3. 1931	W. J. Coxey		ANSP
	male	Peru	Yurimaguas, Huallaga River	5. 4. 1920	H. S. Parish		ANSP
	female	Brazil	Teffe	4. 2. 1920	H. S. Parish		ANSP
	female	Peru	Rio Aguaytis, 300 m	1. 6. 1947	Weyrauch		ANSP
Petasida ephippigera	male	Australia	5 km NNW. Of El Sharana, nr. Pine Creek (N.T)	25. 1. 1973	R. Schodde	K. H. L. & Key 1984	ANSP
	female	Australia	16 km E of Mt. Cahill (N.T.)	7. 3. 1973	K. H. L. & B. Key	K. H. L. & Key 1984	ANSP
Phymateus saxosus	male	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m.	1. 5. 1937	C. Lamberton		ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**

	male	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m.	1. 5. 1937	C. Lamberton		ANSP
	female	Madagascar	high plateaus, Manandriana	0. 11. 1930	Olsoufieff		ANSP
	female	Madagascar	high plateaus, Manandriana	0. 11. 1930	Olsoufieff		ANSP
Zonocerus variegatus	male	Congo	Rd. N1. Manenge to Makaba	10. 6. 1982	M. Donskoff		MNHN
	female	Congo	Rd. N1. Itaba 118 km to Brazzaville	20.6. 1982	M. Donskoff		MNHN
Poekilocerus pictus	male	India	Coimbatore	0. 4. 1932	P.S. Nathan	D. K. McE. Kevan 1962	ANSP
	male	India	Coimbatore	0. 4. 1932	P.S. Nathan	D. K. McE. Kevan 1962	ANSP
	female	India	Coimbatore	0. 4. 1932	P.S. Nathan	D. K. McE. Kevan 1962	ANSP
	female	India	Coimbatore	0. 4. 1932	P.S. Nathan	D. K. McE. Kevan 1962	ANSP
	female	India	Trichinopoly (Madras Pres.)	Fall 1921	C. Leigh		ANSP
Psednura musgravei	male	Australia	Burrill Lake, nr. Ulladula(N.S.Wales)	3. 9. 1948	E. F. Riek	J. A. G. Rehn 1951	ANSP
	male	Australia	Burrill Lake, nr. Ulladula(N.S.Wales)	3. 9. 1948	E. F. Riek	J. A. G. Rehn 1951	ANSP
	female	Australia	"Narrow Neck," Kattomba (N. S. Wales)	4. 12. 1948	K. H. L. & B. Key	J. A. G. Rehn 1951	ANSP
Psedna nana	male	Australia	10 mi. ENE. Of Esperance (W.A)	14. 11. 1969	B. Key & Upton	J. A. G. Rehn 1953, K. H. L. & Key 1971	ANSP
	female	Australia	20 mi. ESE. Of Karragullen (W.A)	5. 11. 1954	J. H. Calaby	J. A. G. Rehn 1953, K. H. L. & Key 1971	ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**

Pseudormorphacris notata	male	Myanmar	Rangoon		F. J. Meggitt	B. Uvarov, D.R. Ragge 1989	BMNH
	female	Myanmar	Rangoon		F. J. Meggitt	B. Uvarov, D.R. Ragge 1989	BMNH
Parasphena imatogensis	male	Sudan	Imatong Mts. (E. E.), 9300 ft	12. 2. 1936	H. B. Johnston		BMNH
	female	Sudan	on short grass at the Imatong Mts. (E. E.),8600 ft	12. 2. 1936	H. B. Johnston		BMNH
Pyromorpha vignaudi	male	Central African Republic	Fort Sibut, 1374 ft	13. 8. 1934	J. A. G. Rehn	C. C. Hsiung 1974	ANSP
	male	Central African Republic	Fort Sibut, 1374 ft	13. 8. 1934	J. A. G. Rehn	C. C. Hsiung 1974	ANSP
	female	Central African Republic	Fort Sibut, 1374 ft	13. 8. 1934	J. A. G. Rehn	C. C. Hsiung 1974	ANSP
	female	Central African Republic	Fort Sibut, 1374 ft	13. 8. 1934	J. A. G. Rehn	C. C. Hsiung 1974	ANSP
Anarchita aptera	male	India	35 Km NW of Palayamkottai	7. 3. 1969	RE. ST R. M. Blackith		ANSP
	female	India	35 Km NW of Palayamkottai	7. 3. 1969	RE. ST R. M. Blackith		ANSP
Zarytes squalinus	male	India	Kodaikanal	12. 4. 1969	RE. ST R. M. Blackith		ANSP
	female	India	Kodaikanal	12. 4. 1269	RE. ST R. M. Blackith		ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
Schulthessia	male	Madagascar	Oriental Forest Dist.	12. 1936 to 4.	C.	Hebard 1924	ANSP

biplagiata			Rogez, betw. Tamatave & Tananarive. 800m	1937	Lamberton		
	male	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m	12. 1936 to 4. 1937	C. Lamberton	Hebard 1924	ANSP
	female	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m	12. 1936 to 4. 1937	C. Lamberton	Hebard 1924	ANSP
	female	Madagascar	Oriental Forest Dist. Rogez, betw. Tamatave & Tananarive. 800m.	12. 1936 to 4. 1937	C. Lamberton	Hebard 1924, D. K. McE. Kevan 1962	ANSP
Mekongiella kingdoni	male	China	Tsela Dzong Tsangpo Valley 10,000ft	24. 12. 1935	Capt. F. Kingdom Ward	B. Uvarov	BMNH
	female	China	Tsela Dzong Tsangpo Valley 10,000ft	24. 12. 1935	Capt. F. Kingdom Ward	B. Uvarov	BMNH
Prosphena scudderi	male	El Salvador	Candelaria	31.8.1955	B. Malkin	H.F. Strohecker	ANSP
	female	El Salvador	Candelaria	31.8.1955	B. Malkin	H.F. Strohecker	ANSP
Rubellia nigrosignata	male	Madagascar	Beheloka	14. 4. 1962	D. Wintrebert	M. Descamps 1966	MNHN
	female	Madagascar	on bge. In Andoharano village, Lake Alaotra	2. 2. 1988	M. Donskoff		MNHN
Sphenarium histrio	male	Mexico	5 mi. N Acapulco, (GRO)	15. 9. 1940	C. Bolivar & H.R. Roberts	W. Boyle 1974	ANSP
Species	**Sex**	**Country**	**Locality City (Region)**	**Date (DD.MM.YYYY)**	**Collector**	**Determined by**	**Museum**
	male	Mexico	ridge, 2 min. N.	15. 9. 1940	C. Bolivar	W. Boyle 1974	ANSP

			Acapulco (GRO)		& H.R. Roberts		
	female	Mexico	ridge, 2 min. N. Acapulco (GRO)	15. 9. 1940	C. Bolivar & H.R. Roberts	W. Boyle 1974	ANSP
	female	Mexico	ridge, 2 min. N. Acapulco (GRO)	15. 9. 1940	C. Bolivar & H.R. Roberts	W. Boyle 1974	ANSP
Tagasta indica indica	male	India	Ledo Road, 1.8 m from Ledo (Assam)	30. 7. 1944	J. W. H. Rehn	Rehn 1953	ANSP
	male	India	Ledo Road, 1.8 m from Ledo (Assam)	19. 8. 1944	J. W. H. Rehn	Rehn 1953	ANSP
	female	China	Mts. 5 mi. S. of Lung-show, Lung cheu Dist. (Kwansgi)	8.8. 1934	Ernest 8. 1934		ANSP
	female	India	Ledo Road, 1.8 m from Ledo (Assam)	19. 8. 1944	J. W. H. Rehn	Rehn 1953	ANSP
Aularches miliaris	male	Thailand	On Musa plant in Lot 1870 (Prachin Buri)	9. 8. 1962			BMNH
	female	Thailand	On Musa plant in Lot 2870 (Prachin Buri)	9. 8. 1962			BMNH
Taphronota ferruginea	male	Cameroon	Lolodorf	4. 2. 1919	J. A. Reis		ANSP
	male	Cameroon	Batangan	0. 2. 1920			ANSP
	female	Cameroon	Batangan	0. 5. 1920			ANSP
	female	Cameroon	Batangan	9. 5. 1920			ANSP